

RECENT ADVANCES IN PLANT GENETICS

By

F. W. SANSOME,

Ph.D., F.L.S., F.R.S.E.

Research Worker, The John Innes Horticultural
Institution, Merton

AND

J. PHILP,

B.Sc., F.L.S.

Research Worker, The John Innes Horticultural
Institution, Merton

With Foreword by

Sir DANIEL HALL,

K.C.B., M.A., LL.D., D.Sc., F.R.S.

Director, The John Innes Horticultural Institution, Merton; Chief
Scientific Adviser to the Ministry of Agriculture and Fisheries

With 56 Illustrations and 42 Tables



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To
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OUR TEACHER AND FRIEND

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FOREWORD

By SIR DANIEL HALL, K.C.B., M.A., LL.D., D.Sc., F.R.S.,
Director of the John Innes Horticultural Institution, Merton;
Chief Scientific Adviser to the Ministry of Agriculture and
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THE science of genetics is comparatively new, for it may be said to have received its first systematic basis on the general recognition of Mendel's generalisations about the beginning of the present century. Mendel's scheme of inheritance, with its insistence on the transmission from generation to generation of parental characters as units, provided a working basis which served to explain many of the facts that had been observed by the breeders of plants and animals. It also served as a guiding hypothesis to such breeders and enabled them to obtain with some degree of certainty desired combinations of characters and to fix the new types. In the earlier years of investigation exceptions were numerous and only slowly yielded to explanation. Much still remains to be understood, but it may be claimed that all the later work goes to demonstrate the general truth of inheritance on mendelian lines.

De Vries extended the theory by demonstrating that "new characters may arise from time to time by "mutations." But the great forward step came with the association of the mendelian characters with the chromosomes of the nucleus, which provided a mechanism on which mendelian inheritance would work and a physical basis for the observed laws of inheritance. In all the more recent work genetical observations are correlated with chromosomal structure and behaviour. Genetics has now become one of the most rapidly developing sciences; the elucidation of the structure of the nucleus is of no less importance than the disclosure of the constitution of the atom. So rapid has progress been that it is difficult for any but professional students to keep in touch with the literature,

scattered as the papers are in many different periodicals. There are several excellent handbooks which set out clearly the prime mendelian basis and its explanation by the chromosome theory of heredity. The present book aims at an exposition of the more recent developments of the theory, more particularly within the last ten years, during which the experimental study of polyploidy has done so much to confirm the general hypothesis. The authors are themselves actively engaged in research and are daily brought face to face with the intricate problems that are presented by any exact study of the breeding of plants. They are appreciative of the applications of investigations of this character to creation of the new varieties of plants required by the farmer and the gardener. In that direction indeed lies the greatest promise of economic progress in the production of food, fibre, and other plant materials. In all countries practical men are seeking to create new varieties, this book will give them an outline of the theoretical basis for their work and may save them from many pitfalls and much wasted effort.

A. D. HALL.

PREFACE

WHILE there are several elementary text-books on plant genetics, there is no recent book in English dealing with the more modern developments of the science. The present book is an attempt to summarise the chief advances made in plant genetics during the last ten years.

In our choice of matter we have subordinated particular aspects to the wide view. Although of necessity we have had to enter in some detail into particular questions of importance, our principal object has been to give the reader a perspective of modern plant genetics, and the manner in which it has developed and is developing. For this reason we have incorporated much of the work on the fruit fly *Drosophila*, which on certain points provides evidence that is meagre or lacking in plants.

Considerations of space have made it impossible to deal at any length with such questions as sex in plants, chimæras, and the mathematics of inheritance and populations. References to the literature on these subjects, however, are to be found in the bibliography.

The book will, we hope, be useful to the honours student in genetics, but we have intended it primarily for the teacher, the research geneticist (applied and purely scientific) and the general biologist. We may express a hope that this *résumé* of work on the plant side may do a little to remedy the unfortunate lack of contact that exists at present between the plant and animal branches of the science. Many of the phenomena dealt with here, like polyploidy, in spite of the fact that they are of great significance for the general theory of genetics, are at present almost completely ignored by zoologists, as the phenomena are largely peculiar to the plant kingdom.

We take this opportunity of acknowledging our indebtedness to the various authors and publishers who have permitted us to

reproduce their figures and tables, and to Sir Daniel Hall, Professor J. B. S. Haldane and our colleagues at the John Innes Horticultural Institution for their help, advice and criticism. Our gratitude is also expressed to Miss D. M. Cayley, Dr. P. Koller, Mr. W. J. C. Lawrence, Mrs. E. Sansome and Mr. L. H. Stone for assistance in proof reading. In conclusion we also wish to thank Messrs. J. & A. Churchill for the manner in which they have placed their experience at our disposal.

F. W. S.

J. P.

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RECENT ADVANCES IN PLANT GENETICS

CHAPTER I

INHERITANCE IN DIPLOIDS

INTRODUCTION

Introduction — Mosses — Mendel's Laws — Fungi — Algae — Ferns — Angiosperms — Gametic Characters — Certation — Incompatibility — Factor Interaction — Xenia — Lethal Factors — Variegation — Extra-nuclear Inheritance—Conclusions.

GENETICS has made a considerable advance in the last decade. This is principally due to a more extensive investigation into various phenomena of heritable variation among diverse organisms, and to an intensive study of particular species, combined with a more general use of recent cytological, mathematical and physiological findings. The progress made in related branches of biological science is strongly reflected in the position taken by genetics at the present day.

The value of investigations amongst widely separated forms is in no way more strikingly illustrated than by the data obtained from experiments with lower plants. In the mosses and ferns there is a well-marked alternation of generations. The gametophytic generation bears the sexual organs. These give rise to the gametes which may or may not be differentiated into sexually dimorphic forms.

The fusion of the gametes, called fertilisation, produces the zygote which initiates the sporophytic generation. This in turn produces spores which give rise again to the gametophytic generation.

The most important part of the gamete is the nucleus. This is constituted of a number of bodies, the chromosomes. The chromosomes undergo changes of appearance throughout their history, but

there is strong evidence that they are continuous autonomous bodies. It is clear that the fusion of two gametes at fertilisation will give rise to a nucleus with the sum of the number of chromosomes contained in the nuclei of these gametes. As the zygote develops, each time the nucleus divides, every chromosome divides, so that the daughter cells have a chromosome complement identical with that of the original zygote cell.

The sporophytic generation thus has, in general, twice as many chromosomes as the gametophytic generation. Immediately before the inauguration of the gametophytic generation, two nuclear divisions take place, but with only one division of the chromosomes. This process, called meiosis, naturally halves the number of chromosomes. As a result, spores produced by the sporophyte or diploid generation contain the chromosome number of the gametophyte or haploid generation, which is half that of the diploid. It should be mentioned in passing, that in plants, the terms sporophyte and diploid, and gametophyte and haploid are not always synonymous.

Where meiosis or, as it is more loosely called, the maturation division or reduction division, follows very shortly after fertilisation as in *Spirogyra*, the sporophytic generation is greatly reduced. Where fertilisation follows shortly after meiosis, as in the Angiosperms, the gametophytic generation is practically confined to the gametes themselves.

Heritable characters must be controlled by determiners, or "factors," which retain their individuality throughout the life cycle and since, in general, only the nucleus is carried on from generation to generation, these factors are presumably carried in the nucleus.

MOSSES

The manner in which characters are inherited has been clearly demonstrated in mosses, where both the gametophytic and sporophytic generations are approximately equal in length and exist for some time. If characters are determined by factors in the nucleus, one expects their inheritance to reflect the life history of the nucleus; at fertilisation the factors of the two gametes will be contained together in one nucleus of the zygote in a double condition, and at meiosis will again assume the single condition in the nucleus.

If there is to be constancy in inheritance, the factors necessarily must not be influenced by their passage through the sporophytic generation, and the characters will be exhibited in the gametophytic generation. Wettstein (1924 a) found that this was the case in mosses. He crossed two races of *Funaria hygrometrica* which differed in several characters, such as size of spore, leaf breadth, division rate of protonema, breadth of the perichætal leaf of the antheridium, shape of the paraphysis cells, form of the sporogonium and capsule colour. Of these, the form of the sporogonium and the capsule colour are sporophytic characters, the rest are characters exhibited

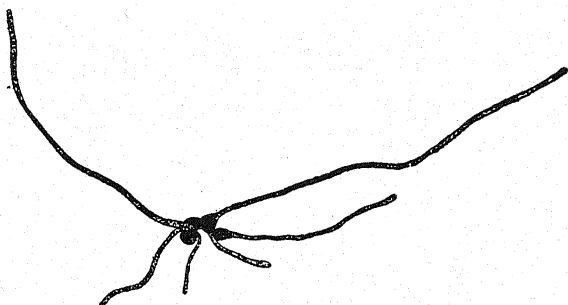


FIG. 1.—*Funaria hygrometrica univalens macrospora* × *microspora*.
Germinating tetrad of spores. × 40. (Wettstein, 1924 a.)

by the gametophyte. The characters were designated as follows and a small letter was used to represent the contrasting or allelomorph character—large spore G, high rate of division in the protonema O, broad perichætal leaf B, shape of the paraphysis cells P, coloured capsule C and form of the sporogonium S. A cross made between two plants having the constitution GOBSCP and gobscp respectively, gave eight identical sporophytes which must have had the constitution GgOoBbSsCcPp. Two hundred spores were isolated and cultured. As a result the proportions of plants of the contrasting types were found to be

B : b 95 : 79
P : p 98 : 76
C : c 92 : 82

Thus the above character pairs, in each case, give a ratio of approximately 1 : 1 which is to be expected if each is controlled by a pair of independent factors carried in the nucleus. As a result of fertilisation, the factor **B** in one gametic nucleus is included with the factor **b** from the other gametic nucleus. A sporogonium and seta are formed and meiosis in the sporogonium again reduces the nucleus from the double to the single condition. The factors are accordingly also separated one from another. The four spores which result from meiosis in the sporogonium of a diploid cell remain together as a tetrad of spores in the moss (see Fig. 1). It is possible therefore to isolate tetrads and so to examine the characteristics of the haploid descendants of a single diploid cell. Wettstein isolated 62 spore tetrads from a hybrid between **GBPC** and **gbpc**, of which 41 germinated and 35 formed mature sporogonia. Examination showed that 24 tetrads gave

16	GBPC	<i>gbpc</i>
5	GBPc	<i>gbpC</i>
2	GBpc	<i>gbPC</i>
1	GbPc	<i>gBpC</i>

and 11 gave

6	GBPC	<i>gbpc</i>
1	GBPc	<i>gbpC</i>
1	GBpC	<i>gbPc</i>
2	GbpC	<i>gBPc</i>
1	GbPc	<i>gBpC</i>

Thus every tetrad contained two types of spores, each type being represented twice. Moreover the types are balanced, so that if one character determiner is present in one type of spore, the alternative factor is present in the other type. It is clear therefore that segregation of one factor from its counterpart (allelomorph) had occurred in the formation of the spores from a diploid cell. Further, of the two nuclear divisions which gave rise to the four nuclei, only one had been associated with the segregation of each factor from its allelomorph. Segregation must have occurred at the first division for all factors, otherwise more than two types of spores would have been possible.

The work on mosses is therefore an experimental demonstration of the laws postulated by Mendel in 1865 as a result of his work on *Pisum sativum*. These laws in Mendel's words (translation from Bateson 1930) are, "the theory is confirmed, that the pea hybrids form egg and pollen cells which in their constitution represent in equal numbers all constant forms which result from the combination of the characters united at fertilisation," and "the relation of each pair of different characters in hybrid union is independent of other differences in the two original parental stocks."

These laws can also be expressed in the terms, "purity of the gamete" and "random assortment of factors in segregation."

The technique of tetrad analysis in mosses and other plants is laborious and so precludes the possibility of obtaining data of statistical value. However, the demonstration that the immediate products of meiosis are qualitatively different in respect of one pair of alternative characters, and that segregation has taken place at one of the two divisions of meiosis, is very important. Further, the resulting spores represented the exact constitution in respect of one character pair of one of the gametes which had helped to create the sporophyte at fertilisation, while the other type of spore contained the allelomorphic factor from the other gamete participating in fertilisation.

The parental types are recovered without contamination by their passage through the hybrid sporophyte. This analysis of tetrad spores, taken in conjunction with the first described experiment of Wettstein where the allelomorphic factors segregate in the ratio 1 : 1 after meiosis, indicates that the diploid nucleus of the sporophyte is reduced to the haploid nucleus of the gametophyte, synchronously with the change from the hybrid constitution of the sporophyte **Xx** to the pure types **X** and **x**. Similar results have been obtained from work on the Algæ and Fungi.

FUNGI

In the Fungi, as in the mosses, it is often possible to isolate the cells resulting from the meiosis of one diploid cell. By this method,

it has been demonstrated that segregation of the factors takes place at meiosis. Some information may be gathered also as to whether segregation takes place at the first or second of the two meiotic divisions.

Phycomycetes. Burgeff (1928) investigated the behaviour of various so-called mutant forms of *Phycomyces Blakesleeanus* when intercrossed and when crossed with the original type. The different forms were piloboloides (*ba*), gracilis (*gra*), mucoroides (*muc*), arbusculus (*arb*) and pallens (*pal*). Each type appears to be controlled by a single factor and all except mucoroides are recessive to the normal form. Various combinations of these factors with the plus and minus sex factors were made.

Where two or more pairs of factors were segregating, it was possible to determine whether or not both factors segregated at the first or second division.

In the case of the heterozygous zygotes (*Arb arb*, + —) it was found that 50% (called tetrakrats) gave four different haploid derivatives having the respective constitutions *Arb* +, *Arb* —, *arb* +, *arb* —, and 50% (called dikrat) gave only two types of derivatives; either *Arb* + and *arb* — or *Arb* — and *arb* +. If the segregation of both pairs of factors takes place at the first division, only two haploid types are expected from each zygote—either *Arb* + and *arb* — or *Arb* — and *arb* +. If the two factors segregate independently the two types should occur with equal frequency. The fact that 50% of the zygotes produce four types of haploids as a result of meiosis indicates that one or both of the factor pairs must segregate at the second division.

Ascomycetes. The study of heterothallism has thrown considerable light on the manner in which the factors segregate. Heterothallism was first discovered by Blakeslee (1904) in certain species of the Mucorales. He showed that in these Fungi there were two strains morphologically alike but physiologically different. One strain must come into contact with the other before sexual reproduction takes place. Blakeslee called the two strains plus and minus respectively, and they have generally been regarded as representing sexually differentiated forms. This phenomenon has since been found in a number of *Ascomycetes* and *Basidiomycetes*. Species

which are differentiated into plus and minus strains are said to be heterothallic, whereas those with no such differentiation, zygospore formation taking place in single spore cultures, are homothallic.

DIAGRAM OF SEGREGATION IN THE ASCOMYCETES.

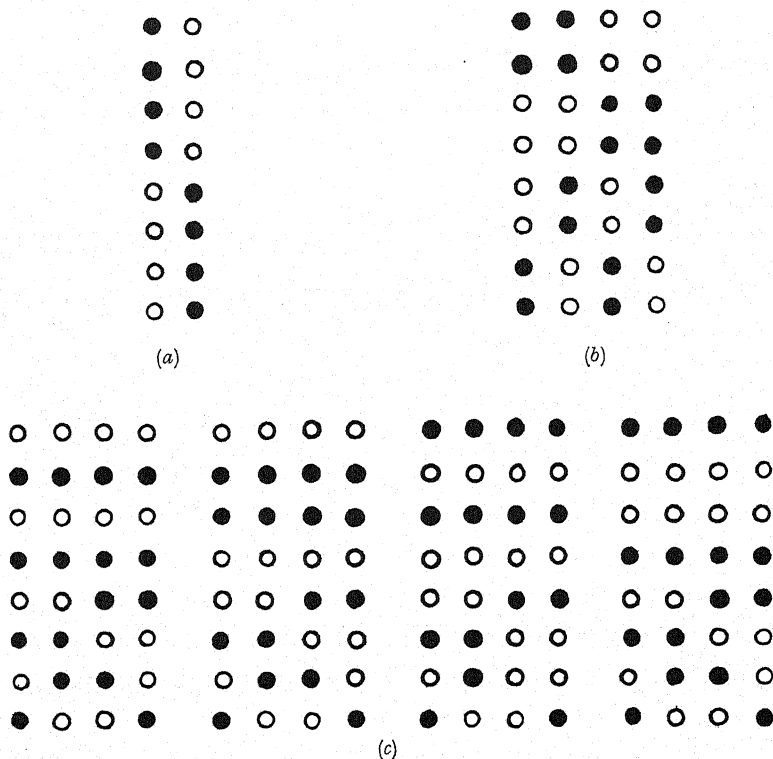


FIG. 2.—Scheme of the position of spores in the ascus of *Neurospora sitophila*, if (a) the first division is reductional; (b) the second division is reductional; and (c) the third division is reductional. (After Dodge, 1927.)

Shear and Dodge (1927) and Dodge (1927, 1928) isolated the eight spores from a single ascus of the heterothallic *Neurospora crassa* and found that four were of one group (plus or minus) and four were of the alternative group. This indicates that segregation of the "sex"

factors takes place in the formation of the ascospores, but it does not indicate at which of the three divisions the segregation occurs.

Dodge made a cytological investigation of *N. sitophila* and found that the spindle axes of divisions 1 and 2 were in a longitudinal direction with regard to the length of the ascus, while that of division 3 was transverse.

Dodge considered the end products of segregation of the factors when it occurred at the first, second or third divisions. The diagram (Fig. 2) shows the different arrangements of spores in the ascus with the three possible types of segregation.

Wilcox (1928) isolated the eight spores which lie in a row in the ascus of *N. sitophila* and identified them according to their position in the row. The plus and minus spores alternated in pairs in each half of the ascus. Here, therefore, the sex factors must have segregated at the second division of the ascus nucleus.

N. tetrasperma (Shear and Dodge) is homothallic and normally forms four large bisexual spores in place of eight unisexual spores. Sometimes two small spores take the place of one large spore. The resulting mycelia from these small spores are heterothallic. About half of the small spore cultures were plus and half were minus strains. Hence the normal large spores were homothallic through containing both plus and minus factors. Dodge (1928) believes that the sex factors probably segregate at the second division in *N. tetrasperma*.

Cayley (1931) investigated the phenomenon of aversion in *Diaporthe pernicioso*. She found that intra-perithecial aversion in which mycelia derived from the spores of one perithecia refused to mix, could be explained by the assumption of two or more pairs of factors which segregated independently of each other and of the sex factors. The results seem to indicate that segregation either takes place at the first or second division of the ascus. These aversion factors are possibly analogous to incompatibility factors in higher plants (see pp. 21-31).

Basidiomycetes. Kniep (1922) found four different strains in *Schizophyllum commune* and *Aleurodiscus polygonius*. He assumes therefore that "sex" is determined by two pairs of factors Aa Bb which segregate in the formation of the basidiospore. Meiosis

occurs in the basidium immediately after fertilisation which takes place by the fusion of the two nuclei of the young basidium. The

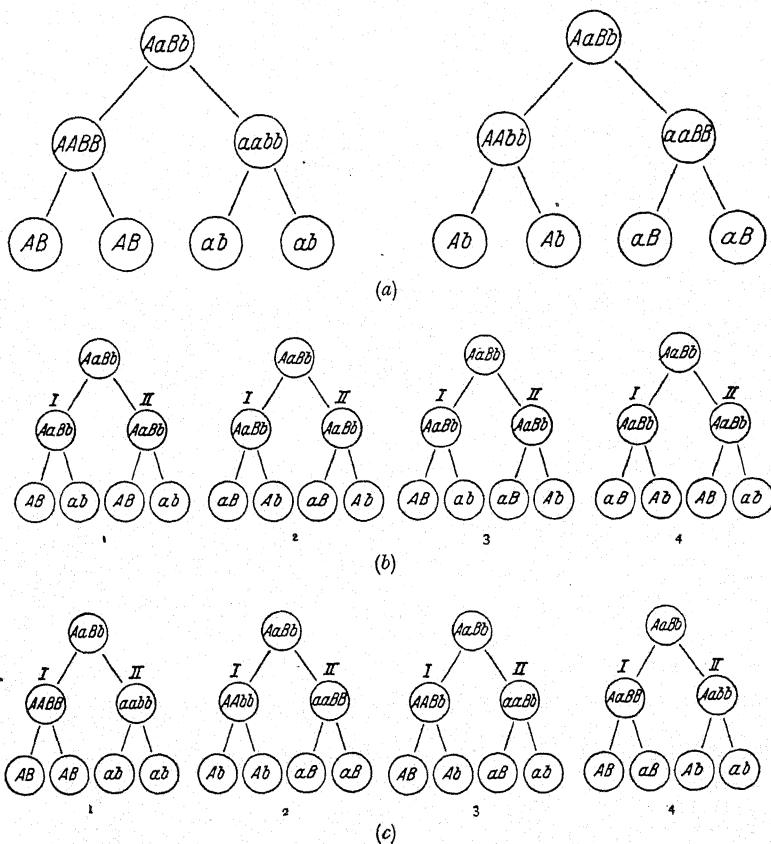


FIG. 3.—Scheme of the segregation of two independent pairs of factors Aa and Bb (a), where the first division of meiosis is reductional; (b) where the second division is reductional; (c) where both factor pairs segregate at the first division (I) and (II), and where one factor pair segregates at the first and the other pair at the second (3) and (4). (Stern, 1928.)

only possible zygote is of the constitution $AaBb$. The spores can be of the constitutions AB , Ab , aB , ab , if the pairs of factors Aa

and Bb segregate independently as is supposed. The four strains will only fuse in such a manner that unlike factors attract and like factors repel one another. Hence fusion will take place between mycelia bearing AB and ab, or Ab and aB, but in no other way.

In *Aleurodiscus*, Kniep found that one basidium gave rise to two types of spores—either AB and ab, or Ab and aB. No basidium produced all the combinations. This indicates that segregation takes place at the first division of meiosis (see diagram, Fig. 3). In *Coprinus lagopus* Hanna (1925) and Newton, D. E. (1926) find that there are three classes of basidia, (1) those which give all four possible combinations, (2) those which give two AB and two ab, and (3) those which give two Ab and two aB. Hanna therefore concludes that segregation of the sex factors takes place at the second of the two divisions in this species.

Funke (1924) came to a similar conclusion with regard to *Hypholoma fasciculare*, *H. capriodes* and *Collybia velutipes*. Newton considers the results in *C. lagopus* to be best explained on two assumptions, (1) that the two sex factors in the nucleus of each spore segregate independently, and (2) that in some basidia the segregation of both sex factors takes place at the first division, and in the other basidia the segregation of one pair of factors takes place at the first division and the other pair at the second. A third possibility, as Hanna concludes, that both pairs of factors segregate at the second division, must not be neglected.

Newton also investigated *C. Rostrupianus* in which sex was controlled by one pair of factors. By observing the sex of basidiospores, whose position in the basidium was known, she was able to show that segregation of the sex factors sometimes took place at the first and sometimes at the second division of meiosis in this species. The first division will produce two cells while the second division of these two cells will produce four cells which are orientated at right angles to the first division spindle. Hence if segregation takes place at the second division one expects that sometimes the spores at opposite corners of the basidium will be similar in constitution (see Fig. 3).

Brunswik (1924) in *Coprinus curtus*, *C. deliquescens*, *C. ephemerus*

and *C. fimetarius* also found more than two apparent sex forms, but suggested that in some cases the Fungi were potentially bisexual, and fusion was controlled by one or two pairs of self incompatibility factors.

Brunswick analysed 93 tetrads of *C. fimetarius* (*lagopus*) with the following results :—

37	gave	four	different	types	of	spores	AB, Ab, aB and ab
29	„	two	„	„	„	AB and ab	
27	„	„	„	„	„	Ab and aB	

This indicates that the two factors may segregate independently and that segregation can take place either at the first or the second division of meiosis.

Ustilaginales. Dickinson (1931) isolated the four spores of known position in the promycelium of *Ustilago lævis*. The behaviour of the two factors **A** and **B** for sexual fusion as well as the two alternative character pairs (cream *vs.* brown and corrugated *vs.* depressed) were investigated. Utilising the same methods as illustrated above, each character was found to segregate either at the first or at the second division of meiosis.

The work on the Fungi with the results obtained in mosses supports the view that segregation of the hereditary factors takes place during the meiotic divisions of the nucleus which inaugurate the gametophytic generation. It has also been shown that the factors may segregate from one another at either of the two divisions and not necessarily at that division which reduces the chromosome number from the diploid to the haploid state. Wilcox showed that in *Neurospora sitophila* the "sex" factors segregated regularly at the second division, but in most other cases it has been found that factors may segregate at either division. Reference should be made to p. 189 for an explanation of this phenomenon in the light of recent work on higher plants.

ALGÆ

The *Spirogyra* plant is haploid. Fertilisation consists in the migration of the nucleus from one cell of the thread of one plant into that of an adjoining cell of another plant, and the subsequent

fusion of the two nuclei (*cf.* Saunders, H., 1931). Meiosis follows immediately, giving rise to four nuclei, only one of which survives and gives rise to a daughter plant.

Transeau (1919) found that the two wild species *Spirogyra communis* and *S. varians* differed in respect of (1) the size of the zygote and (2) the size of the cell which carried the zygote, as well as (3) the angle at which the zygote was placed in the cell. He crossed these two species and found that the characters were inherited independently. Combinations of these characters which did not appear in the parents were found in the progeny. Further, these characters were found to be pure, or, in other words, although the characters of the two species had been associated in a hybrid zygote, the spores of that hybrid contained only one of each pair of characters corresponding exactly to the same character of one of the parents. Pascher (1916, 1918) crossed two cells of *Chlamydomonas*, which is also haploid throughout most of its life history, and analysed the four haploid cells resulting from the division of the zygote. In five cases he found that two of the four cells had the character of one parent and the other two cells had the character of the alternative parent. Further, where two or more characters were involved, he found that contrasting characters separated into the two cells independently of every other pair of contrasting characters.

The technical difficulties of analysis of algæ prevent full investigations of segregation of characters, but the above experiments agree as far as they go, with Wettstein's work on mosses, in showing that the factors which determine heritable characters are segregated at the formation of the gametophyte, and that the factor contributed by a parent is transmitted through the gametes of the plant to the succeeding generations without loss of individuality. The idea of the purity of the gamete has been symbolised by German geneticists in the expression "personified gamete." By this they imply that the haploid plant (gametophyte) cannot be of hybrid or "mixed" structure, but only contains one representative of each allelomorphic factor as distinct from the diploid (sporophyte) which contains two representatives. This phrase applies to normal diploid organisms, but later a more accurate description will be given (see p. 207).

FERNS

Meiosis takes place in the sporangia of ferns. The resulting spores each gives rise to a prothallus which is the gametophyte generation (haploid). The archegonia and antheridia are formed on the prothallus, where fertilisation takes place and the young fern plant develops. Since in the ferns on which genetical experiments have been made, one prothallus forms both antheridia and archegonia, self-fertilisation will give rise to sporophytes which are homozygous for all characters carried as factors in the nuclei of the prothallus.

Andersson-Kottö (1927) bred from one plant of *Polystichum angulare* and found after random cross-fertilisation of the resulting prothalli, that the next sporophytic generation segregated in respect of two factors controlling the development of the frond. Four types of frond, types (1.2.3.4) were found in the ratio 9:3:3:1. By sowing the spores of each sporangium separately she showed that segregation was alike and random in each sporangium. By cultivating the prothalli from each spore in isolation, it was found that all the sporophytes from the self-fertilisation of one prothallus were identical and pure (homozygous) for those characteristics. Andersson-Kottö counted the gametophytes which gave rise to the different types of sporophytes by self-fertilisation. Twenty-two gave type 1 sporophytes, 20 gave type 2, 18 gave type 3 and 18 gave type 4. This agreement with the expected 1:1:1:1 ratio is close, and indicates that the two pairs of allelomorphic factors segregate independently in the sporangium of the hybrid sporophyte. If we call *Aa* and *Bb* the two pairs of allelomorphic factors, we can follow them through the life history. The hybrid sporophyte will be of the constitution *AaBb* and will give rise to the four types of gametophytes *AB*, *Ab*, *aB* and *ab* in equal proportions. These, on selfing, will only give rise to sporophytes *AABB*, *AbAb*, *aBaB* and *abab* respectively. If, however, these four gametophytes are crossed, there are sixteen possible types of matings. These are illustrated in the chequerboard (Fig. 4), and may also be found by multiplying (*1AB : 1Ab : 1aB : 1ab*) by itself algebraically, *i.e.*, the zygotic combinations from random pairing of the genetic constituents.

Analysis of Fig. 4 shows that there are nine types of zygote where both A and B are present, three where A is present and not B, three where B is present and not A, and one where neither A nor B is present.

After cross fertilisation of the gametophytes, four types of sporophyte, in the ratio 9:3:3:1, were obtained. This is in agreement with expectation. Further analysis of Fig. 4 shows that both A and a are present in some zygotes, and yet apparently

	CR	Cr	cR	cr
CR	CCRR	CCRr	CcRR	CcRr
Cr	CCRr	CCrr	CcRr	Ccrr
cR	CcRR	CcRr	ccRR	ccRr
cr	CcRr	Ccrr	ccRr	ccrr

FIG. 4.—Dihybrid segregation.

the expression of the plant is that associated with AA. This phenomenon of dominance, where one factor has a greater effect on the expression of the character than its allelomorph, is widespread among plants.

ANGIOSPERMS

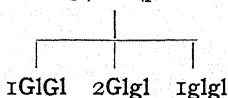
In Angiosperms, the gametophyte is much reduced, the haploid generation being of short duration in the life cycle. It consists of the contents of the pollen grain and tube and the embryo-sac respectively. Consequently it is expected and found that variation in character expression of the pollen tube and embryo-sac is not great in any species. There are, however, several phenomena which indicate that the gametophyte carries a complement of genetic

factors which may have an effect on the characteristics of the haploid generation.

Inheritance of Pollen Characters. These are of two classes, (1) differences in morphological characters, and (2) differences in physiological reactions, *e.g.*, different growth rates of pollen tubes within one style.

Parnell (1921) discovered that pollen of different races of rice, *Oryza sativa*, varied in respect of the storage material. One race has a reserve material of starch while another has a carbohydrate which, although similar to starch, does not give the starch reaction with iodine. The starchy race has starch both in pollen and endosperm, while the non-starchy race has a glutinous endosperm which does not contain a true starch. Both Parnell and Chao (1928 *a*) found that a hybrid between starchy and non-starchy races produced equal numbers of starchy and non-starchy pollen grains. The observed results obtained by Chao were 3,179 starchy: 3,151 non-starchy pollen grains. This 1:1 ratio affords good evidence that these characters depend upon the independent assortment of a pair of allelomorphic factors at the preceding meiosis. These factors Chao calls **G1** and **g1**. Self-fertilisation of such hybrid plants produced 57,925 seeds,* of which 44,043 had starchy endosperm which stained blue in iodine, and 13,882 had glutinous endosperm. This ratio of 3:1 is the typical mendelian ratio arrived at by random mating between eggs, 50% of which are carrying starchiness and pollen, 50% of which carry non-starchiness. The mating can be symbolised thus:—

$$(\text{eggs } 1G1 : 1g1) \times (\text{pollen } 1G1 : 1g1)$$



The dominance of **G1** over **g1** in expression of type of endosperm results in the two heterozygous plants **G1g1** being included along with the homozygous starchy plants **G1G1**.

Several lines of investigation have led Chao (1928 *a*) to the

* The term "seeds," although not botanically accurate, is used for convenience throughout this book.

conclusion that the recessive factor *gl* affects pollen tube growth in the style. The effect of this factor is influenced by environmental factors. The ratio of dominant to recessive characters in the progeny is therefore sometimes distorted. Thus one plant which gave 21.96% glutinous grains in place of the expected 25% in the first crop gave 30.72% in its sixth crop. Seasonal infertility in rice depends on the environment. With seasonal infertility there is a parallel increase in the percentage of glutinous grains.

Brink and McGillivray (1924), and Demerec (1924 *a*), independently showed that the pollen of a race of maize called waxy (*wxwx*) because of the texture of the endosperm, might be distinguished from that of the non-waxy (*WxWx*) by the starch reaction to iodine. The non-waxy pollen grains give the typical blue colour, while the waxy pollen grains are red in iodine.

From an F_1 heterozygous plant (*Wxwx*), resulting from a cross between these two races both types of pollen are produced in the ratio 1 : 1. Demerec gives the figures 3,437, blue-staining grains, and 3,482 red-staining grains, while Kieselbach and Petersen (1926) give further counts of 13,014 blue-staining grains, and 13,229 red-staining grains. In percentages, Kieselbach and Petersen's results are 49.59% blue and 50.41% red.

A haploid nucleus of the pollen grain fuses with a diploid nucleus of the embryo-sac to form the endosperm. If endosperm characters are determined by factors carried in the nucleus, an experiment can be devised to show the expression in the endosperm of the factors carried in the pollen grain.

Kieselbach and Petersen fertilised a pure waxy maize plant (*wxwx*) with pollen from an F_1 hybrid (*Wxwx*) of non-waxy \times waxy plants. The ovules all carry the factor for waxy (*wx*), therefore the ratio of pollen grains carrying waxy (*wx*) to those carrying non-waxy (*Wx*) will determine the ratio of the two types of endosperm.

Samples from all the pollen used were tested by the iodine method to ensure that pollen from a heterozygote was being used. The result of the experiment on 18,549 maize seeds was that 51.5% of the seeds had waxy endosperm and 48.5% had non-waxy endosperm. The above authors summarised the results obtained by Kempton, Bregger and Brink on endosperm segregation, and showed that from

293 ears of maize, 39,173 out of 79,381 grains had waxy endosperm, *i.e.* 49.3% waxy : 50.7% non-waxy. If we cross two heterozygous plants of the constitution $Wxwx$, we obtain the F_2 generation. Since the female plant is now heterozygous, it will give equal numbers of waxy and non-waxy ovules. The non-waxy ovules will give rise to non-waxy endosperm whatever the type of pollen used, since Wx is dominant to wx . The waxy ovules will behave as in the former case, giving waxy endosperm with waxy pollen and non-waxy endosperm with non-waxy pollen. Therefore 75% of the progeny from these F_1 plants will have non-waxy endosperm and 25% will have waxy endosperm, *i.e.*, 3 : 1 ratio. This example is particularly useful in showing the result of segregation of waxy from non-waxy in the formation of these pollen grains, and the result of recombination of the factors at fertilisation. In both segregation and recombination the factors behave according to the laws of chance.

The numbers estimated in the above experiment were 36,523 waxy grains out of a total of 152,871, or 23.9% waxy in 356 ears. It will be noticed that both in this cross and in the previous one there is a deficiency of grains with waxy endosperm : where 50% was expected 49.5% was obtained, and where 25% was expected 23.9% was obtained.

Various authors have put forward hypotheses to account for these differences. All agree in suggesting that the growth in the style of the pollen tubes carrying the factor for waxy and for non-waxy respectively is different. Brink (1924, 1925), and Brink and McGillivray (1924), showed that the cross, waxy \times heterozygous non-waxy gave a lower proportion of waxy endosperms than the reciprocal cross. They have also shown by desiccation and other methods that the pollen tubes containing non-waxy and waxy exhibit different physiological reactions. Brink (1929 *a*) finds that the extracts of waxy pollen tubes have less diastatic activity than extracts of non-waxy pollen tubes.

The styles of maize show a gradation in size from the top to the bottom of the ear. Brink and Burnham (1927) found that the upper and lower halves of the ear, when pollinated by pollen from a $Wxwx$ plant, gave the same percentage of waxy endosperm. They were therefore led to the conclusion that in the early stages the two

types of pollen grew at different rates, but in later stages at the same rate. The style contains sugars but the pollen contains starch or a starch-like carbohydrate, and the two types of pollen differ in the rate at which their extracts hydrolyse starch. This suggests that in the early stages the pollen tubes containing the non-waxy factor **Wx** differ in their physiological reactions from those containing the waxy factor **wx**, and that this is reflected in their growth rate. When all the starch reserve in the pollen is used up, both types of pollen tubes will absorb sugars from the style, and consequently the rates of growth at the later stages will not be affected by the difference in diastatic activity.

Mangelsdorf and Jones (1926) pointed out that in Kempton's data (1919) certain F_1 plants of maize, when selfed, gave the expected proportion of waxy : non-waxy progeny, but that others gave lower proportions of waxy than was expected. If plants which give the normal ratio are designated as N plants, and those which give a lower proportion of waxy as L plants, the following crosses can be made: $L \times N$, $L \times L$, $N \times L$ and $N \times N$. Kempton's results showed that $L \times N$ and $N \times N$ gave 25.1% and 25.4% of waxy grains respectively, but $N \times L$ and $L \times L$ gave 22.9% and 22.6% respectively when the expected in every case was 25%.

Thus, when N plants were used as male parents, the progeny gave results close to theoretical expectation, but when L plants were used as males the progeny gave 22.6% of waxy; a deviation from expectation of 5.8 times the probable error. It is presumed by the authors, therefore, that an accessory factor is sometimes coupled to waxy, which reduces the number of waxy-carrying pollen tubes affecting fertilisation. This had also been suggested by Brink and McGillivray (1924).

Mangelsdorf and Jones (1926) found that the factor **de** causing defective seeds in maize was linked to **Ga**, a factor which speeds up pollen tube growth. The result of another series of experiments relating to plants with sugary endosperm have been brought into line with those of **de** by East and Hayes (1911), Jones (1924) and Emerson (1925). Owens (1902) found that the F_2 of the cross "Rice pop" \times sugary always had too few grains with sugary endosperm; generally there were 16.2% instead of 25%. Control

crosses showed that when the homozygous dominant **Su Su** (cornaceous) was crossed with the heterozygote **Susu** there was a large excess of **SuSu** plants in the progeny. When the female parent was **susu** there was no marked deviation from the expected ratios. Jones (1924) concluded that there was apparently an interaction between the pollen tubes and the stylar tissue such that pollen tubes carrying the dominant factor **Su** were more able to accomplish fertilisation than the pollen carrying its recessive allelomorph **su**. This only occurs in a sporophyte which also has the dominant factor present either in the homozygous or heterozygous state.

Brink and Burnham (1927) showed that the sugary factor **su** might exert a differential action on **Wx** and **wx** pollen, leading to marked deficiencies in the waxy:non-waxy ratio. This occurs only when the pollen parent is **susuWxwx**, and not when doubly heterozygous **SusuWxwx**. To account for the different reactions between homozygous **susu** plants and heterozygous **Susu**, the authors suggested that **susu** plants exerted a cytoplasmic influence on the pollen tubes, retarding the growth of **wx** pollen tubes as compared with **Wx**. It is interesting to note that Brink does not find differences in diastatic activity between **Su** and **su** pollen as he did between **Wx** and **wx**.

Mangelsdorf and Jones (1926) show that **Ga**, **Su** and **de¹** are linked together and that the peculiar behaviour of **Su** and **de¹** is due primarily to their relationship to **Ga**. They therefore brought into line the factor for defective seeds **de¹** and **Su** which also gives a reduced number of recessives 19.8%.

Certation. Heribert-Nilsson (1920) found that reciprocal crosses in *Oenothera Lamarckiana* between red-nerved plants **Rr** and non-red-nerved plants **rr** gave different proportions of the two types. **Rr** × **rr** gave a ratio of 1 : 1 (181 : 174) as expected, while an excess of red-nerved plants appeared in the reciprocal cross, 254 : 93. He suggested that the pollen tubes carrying **R** grew faster than those carrying **r**. This competition in growth of the pollen tubes of different genetic type he named *certation*. He also found that the difference in rates of growth of the two types was influenced by external environmental factors such as temperature. Davis (1926),

using F_1 plants from the cross *Oenothera Lamarckiana* \times *O. Nanella brevistylis*, which were heterozygous for the factor for red-nerved R, decapitated the style at various intervals of time after pollination. He found a ratio of 1 Rr : 5 rr when the styles were cut off 23 hours after pollination and 1 Rr : 2.8 rr after 27 hours. Davis shows that the pollen of the mutant *Oenothera brevistylis* is slower in growth than that of *O. Lamarckiana*, while Hiorth (1926) reports several crosses in the genus where differences in pollen tube growth are found (see p. 279). Sirks (1926 b) obtained similar differences in ratios of *Datura*, involving the characters purple-white armed inermis.

In *Melandrium*, Correns (1918, 1921) found that pollination with few pollen grains gave 50% of males in the progeny, but with much pollen the average percentage was 35% males. Certation between the male and female determining pollen tubes appears to be the cause of this difference. Where much pollen was applied, the female determining pollen tubes achieved fertilisation more often than the male determining pollen tubes.

This difference in growth rate was confirmed by Correns by another method. He found that the seed from the upper or stylar half of the ovary gave 32% males while the lower half gave 45% males. This indicates that the ovules nearest to the base of the style were fertilised by the faster growing female determining pollen tubes, thus forcing the male determiners to travel further down the ovary to reach an unfertilised ovule. Further, by cutting off the styles at a definite time after pollination, Correns showed that more females were obtained in the progeny. This again supports the view that the nucleus of the female determining pollen grain reaches the ovule more quickly than that of the male determining grain.

If the pollen grains of *Melandrium* are either exposed to alcohol vapour, or allowed to age by keeping, there is a larger mortality of the female determining grains than of the male determiners. Similar results were found by Correns, in *Rumex acetosa* while a considerable number of examples of certation are to be found among the later described aneuploids (see p. 255).

Nilsson Ehle (1911 b) in wheat, Bateson and Sutton (1919) in begonia, Saunders (1928 a), Frost (1915), Snow (1924, 1925),

Waddington (1929) and Philp and Huskins (1931) in stocks, have found further examples of certation.

Dimorphism of Pollen. The contents of the pollen grains in several species differ in a genetical manner. For example, Renner (1919 *a, b*) showed that the shape of the starch in the different pollen grains of some *Oenothera* species was different. *Oenothera curvivelutina* (*Lamarckiana* \times *muricata*) has two types, one (*Lamarckiana*) (see p. 277) having large spindle-shaped starch grains and the other (*muricata*) with smaller, thicker, blunt-ended starch grains.

Strasburger (1910) found that the pollen grains of *Elodea* remained together in tetrads so that he was able to obtain the four pollen grains which arose from the division of one pollen mother-cell. The male plant of *Elodea* is dimorphic in respect of the sex chromosomes (Santos, 1924) and produces two kinds of pollen—a male determining and a female determining. By pollinating a stigma with one tetrad, Strasburger showed that the progeny segregated into two males and two females and that never more than $n/2$ females or $n/2$ males resulted from n tetrads. He therefore showed that segregation of sex determiners occurred during the formation of the pollen grains.

Santos (1924) found that there were two larger and two smaller pollen grains to each tetrad which corresponded to the male and female determining pollen grains of *Elodea* respectively.

Bimodal curves for size of pollen grains have been found in *Cannabis sativa* (Sinoto, 1930), *Melandrium* (Tischler, 1925), and *Rumex acetosella* (Sinoto, 1930) among others (see Sinoto, 1930). These plants have sex chromosomes and the authors correlate the two sizes of pollen grains with the fact that segregation of sex determiners by means of sex chromosomes takes place during the reduction division in these plants.

SELF-INCOMPATIBILITY AND CROSS-INCOMPATIBILITY

De Vries (1906) was the first to find intra-sterile inter-fertile groups of plants within a species—*Linaria vulgaris*. Among other species where similar intra-sterile inter-fertile groups are found are *Antirrhinum hispanicum*, Baur (1919), *Petunia violacea*, Shull (1924) *Capsella Bursa-pastoris*, Shull (1926) and Kikuchi (1926, 1929),

Reseda odorata, Compton (1912, 1913), *Brassica oleracea* var. *capitata*, Detjen (1927) and Kakizaki (1930), *Veronica syriaca*, Filzer (1926) and Lehmann (1926), *Verbascum phoeniceum*, Sirks (1926 a), *Cardamine pratensis*, Correns (1913), Baur (1924) and Beatus (1929, 1931), *Nicotiana*, spp. East and his co-workers (1917-1928), *Prunus*, spp. and *Pyrus Malus*, Crane and Lawrence (1923-1932).

In the case of incompatible pollinations it has been found that either the pollen tube grows so slowly that it is unable to reach the ovule before the flower withers, or the growth of the pollen tube is completely inhibited.

Through the independent work of East and Mangelsdorf (1926), Lehmann (1926), and Sirks (1926 a) on species of *Nicotiana*, *Veronica* and *Verbascum* respectively, the oppositional factor hypothesis for incompatibility was placed on a sound basis. The hypothesis had been suggested by Prell (1921) in a paper surveying the work of others. East and his co-workers (1925-1929) independently put forward the same hypothesis, and credit must be given them for providing extensive evidence of the validity of the oppositional factor hypothesis.

Oppositional Factor Hypothesis. The work of East and Park (1917) on crosses between *Nicotiana Tabacum* and *N. Sanderae* showed that there were three intra-sterile, inter-fertile groups x , y and z . All plants in each group were found to be self-sterile and intra-sterile, but plants of different groups were inter-fertile. A cross between group x and group y gave an F_1 , consisting of equal numbers of plants belonging to groups y and z , while the reciprocal cross $y \times x$ gave equal numbers of z and x plants. It is significant that one of the classes in each F_1 corresponds to that of the male parent. East and Mangelsdorf (1926) put forward the suggestion that this behaviour is governed by a multiple allelomorphic series of incompatibility factors, and that pollen tubes carrying an incompatibility factor will not function properly in stylar tissue having the same incompatibility factor.

The assumption is made that plants of group x have the factors S_1S_3 , plants of group y have S_1S_2 , and plants of group z have S_2S_3 . In the cross $x \times y$, ($S_1S_3 \times S_1S_2$) only S_2 pollen tubes are

normally able to bring about fertilisation. Consequently this cross produces z (S_2S_3) and y (S_1S_2) groups in equal numbers. In the reciprocal cross $y \times x$, ($S_1S_2 \times S_1S_3$) only S_3 pollen tubes function, therefore the progeny consists of x (S_1S_3) and z (S_2S_3) groups in equal numbers (see Fig. 5).

By pollinating in the bud stage it is sometimes possible to obtain seed from normally incompatible pollinations. This may be explained in either of two ways. Either the inhibition of pollen tube growth is less intense at the bud stage, or the greater length of time between pollination and the withering of the style allows the

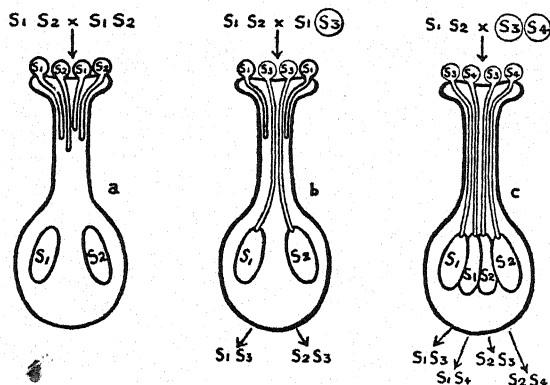


FIG. 5.—Compatible and incompatible pollinations. (Crane and Lawrence, 1929.)

slow growing pollen tubes to reach the ovules. Four plants of the constitution y (S_1S_2) were selfed in this manner and gave progeny of 14 S_1S_1 : 81 S_1S_2 : 38 S_2S_2 plants. The homozygous plants S_1S_1 and S_2S_2 when selfed in the bud bred true, and when normally pollinated with pollen from S_1S_2 plants gave only S_1S_2 plants.

The cross $S_1S_1 \times S_2S_2$ produces offspring of the S_1S_2 class. This class is incompatible when used as a female in crosses with either parent, but may be used successfully as male parent with either. In each case it gives progeny of the S_1S_2 type due to the functioning of pollen tubes carrying unlike factors. Similarly the cross $S_1S_1 \times S_1S_2$ will be fertile, giving S_1S_2 progeny, while the reciprocal cross will be incompatible.

Later Brieger and Mangelsdorf (1926) found that the multiple allelomorphs S_1 , S_2 and S_3 were linked with a factor C which controlled the development of colour in the flower, seed, and stem. The cross-over percentage in one plant, estimated from its progeny of 576 plants, was $24.5 \pm 1.2\%$ on the male side and $18.2 \pm 1.1\%$ on the female side. In another plant the cross-over percentage was 16.2% on the male side and 14.5% on the female side, estimated from a progeny of 220 plants.

Fifteen incompatibility factors in this allelomorphic series have so far been found, and hence an increased number of inter-fertile intra-sterile groups. The different factors have noticeably different degrees of reaction. For example, S_3 in the homozygous condition tends to be lethal, causing the plants to be dwarf with wrinkled leaves and abnormal growth and to be practically male sterile (East, 1930).

Homozygotes of some factors may be obtained with comparative ease, whereas other factors are difficult to obtain in the homozygous condition.

East and Yarnell (1929) and East (1932) have found that there is a fertility factor S_f , which is a member of this allelomorphic series. Plants having the constitution $S_f S_x$, where S_x is any other factor of the series will be self-fertile, and on selfing will only give self-fertiles of the constitution $S_f S_f$ and $S_f S_x$.

$S_f S_x$ plants may be crossed with any self incompatible plant of the species and consequently self-incompatibles together with self-compatibles will appear in the progeny. Anderson and de Winton (1931) found another allelomorph S_F which is able to inhibit the pollen tubes carrying the S_f factor.

Filzer (1926) and Lehmann (1926) independently put forward a similar hypothesis to explain the data in *Veronica syriaca*. All plants are self-incompatible. Seventeen individuals were crossed in all possible ways, and were found to fall into four intra-sterile, inter-fertile groups consisting of seven, five, three and two individuals respectively. Intercrossing plants of any two groups produced plants of two groups in equal numbers, except in one case, where all four groups were obtained. If the four groups A, B, C, D were determined by four factors S_1 , S_2 , S_3 , S_4 (the authors, however, use

Compatible and Incompatible Crosses in Cherries
(Crane and Lawrence, 1931)

$S_3 S_4$ Gov. Wood. X Big d' Schrecken. Gov. Wood.		$S_1 S_4$ Gov. Wood.	$S_3 S_4$ Turkey Heart. Elton.	$S_2 S_3$ Big Napoleon. Emp. Francis. Big Kentish.	$S_1 S_3$ Big de Schrecken. Belle Agathe. Waterloo.	$S_1 S_2$ Bedford Prolific. Black Tartarian B. Early Rivers. Knight's E. Black.	+ Q
41							Bedford Prolific.
47							Black Tartarian B.
51							Early Rivers.
54							Knight's E. Black.
43							Big de Schrecken.
44							Belle Agathe.
45							Waterloo.
46							Big Napoleon.
48							Emp. Francis.
49							Big Kentish.
50							Turkey Heart.
52							Elton.
56							Gov. Wood.
57							41
125							47
126							51
122							54
127							43
128							44 Big d'
129							45 Schrecken.
130							46 X
314							48
320							49 Gov. Wood.
226							50
227							52
536							56
542							57
548							125
549							126
550							122
551							127
555							128

Since the above table was published, Crane and Lawrence have found that $S_x = S_5$ and Turkey Heart probably does not carry both S_3 and S_4 .

the symbols a_1, b_1, c_1, d_1) then A is S_1S_3 , B is S_2S_4 , C is S_1S_4 , D is S_3S_4 , and the cross $A \times B$ will give plants of all four groups, while every other type of cross will give two groups.

Crane and Lawrence (1923-1932) have shown that all varieties of sweet cherries are self-incompatible and fall into nine intra-sterile inter-fertile groups. Reciprocal crosses between varieties of one intra-sterile group are sterile. The authors point out that the results are amenable to East and Mangelsdorf's hypothesis of "incompatibility" factors. By intercrossing varieties of different groups it has been shown that some groups have a factor in common. For example, the cross Biggarreau de Schrecken of group 2 with Governor Wood of group 6 gave two intra-sterile inter-fertile groups in the progeny, one of which fails with the male parent, Governor Wood. Hence, it can be assumed that Big. de Schrecken is of the constitution S_1S_3 and Governor Wood S_1S_4 . Similar results indicate that group 1 is S_1S_2 , group 2 is S_1S_3 , group 3 is S_3S_5 , group 4 is S_2S_3 and group 6 is S_1S_4 (see Table 1).

In the sour cherries, which are tetraploid, and plums which are hexaploid, partially self-compatible varieties are known as well as self and cross incompatible varieties. In the plums complete self-compatibility is also found. The results of Crane and Lawrence afford strong evidence that a hypothesis similar to that of East and Mangelsdorf is applicable to these phenomena in these polyploid fruits, but that the nature of these plants increases the complexities of behaviour. When pollen tubes carrying S_1 will not grow down S_1S_2 styles it is difficult to say what the reaction of pollen tubes with $S_1S_1S_2$ factors will be in a style of the constitution $S_1S_1S_2S_2S_3S_3$, a situation which is possible in the hexaploid plums. Grades of self-incompatibility, together with a considerable proportion of one-way incompatibility, are to be expected in tetraploid and hexaploid species. For example, the hypothetical cross $S_1S_1S_2S_2 \times S_1S_1S_2S_3$ may be compatible as a result of the pollen bearing S_3 with one other factor, but the reciprocal cross may be expected to be incompatible.

Sirks applied the oppositional factor hypothesis to explain incompatibility in *Verbascum phoeniceum*, but found one-way incompatibility to be frequent. Crane and Lawrence suggest that

since the chromosome number of *V. phoeniceum* is 32, it is possibly a tetraploid. If this is indeed the case the polyploid nature of the species is a sufficient explanation of the phenomenon.

Apples vary in their degree of self-compatibility, but only two varieties are possibly completely self-incompatible. Crane and Lawrence (1930 *a*), and Darlington and Moffett (1930) showed that the apple was a secondary polyploid. Instead of containing 17 non-homologous chromosomes in the haploid set, the apple contains four sets of two homologous chromosomes and three sets of three homologous chromosomes. The primary basic chromosome number is presumably seven, *i.e.*, there are only seven different types of chromosome present in the haploid set, but all are repeated more than once (see p. 235). We therefore expect the apple to behave like a complex polyploid in its mode of inheritance. The self and cross incompatibility results appear to be of this nature.

	Number of varieties tested.	Percentage of varieties com- pletely self- incompatible.	Percentage of varieties com- pletely cross- incompatible.
Cherries ($2n = 16$) . .	40	100	70
Plums ($6n = 48$) . .	53	40	13.5
Apples			
Secondary diploid—see p. 234. ($2n = (3 \times 6 + 4 \times 4)$).	42	4.8	4.8
Secondary triploid—see p. 234. ($2n = (3 \times 6 + 4 \times 4\frac{1}{2})$).	5	0	0

Table 2. Showing inverse correlation between chromosome number and complexity, and the frequency of incompatibility (after Crane, 1932).

Kakizaki (1930) obtained some interesting results from experiments with the cabbage. Here there are two types of self-incompatible plants; one which gives only self-incompatible progeny, and the other which segregates into self-compatible and self-

incompatible progeny in a ratio of 1 : 3. Self-compatibles always segregate again into two types in a ratio of 50% self-incompatible : 50% self-compatible. Certain matings between two self-compatible plants are reciprocally incompatible, and between self-compatible and self-incompatible plants some matings are compatible only when the former is the female parent and in other matings when the latter is the female.

These facts obviously cannot be explained by East and Mangelsdorf's hypothesis alone. Kakizaki suggests that besides the oppositional allelomorphic series of *S* factors there are sympathetic factors T_1 and T_2 which influence the pollen tube growth in the style. The *S* series is supposed to be epistatic over the *T* series, but *T* in double dose is more active than an *S* factor in single dose. For example, $S_1S_1T_1T_1$ would be self-incompatible, since S_1 is in equal dosage to T_1 and is epistatic over T_1 . In $S_1S_2T_1T_1$, T_1 would cause the plant to be self-compatible. Some of the self-compatible plants would have the constitution $S_1S_3T_1T_1$ and would segregate on selfing into

1 $S_1S_1T_1T_1$ self-incompatible
 1 $S_3S_3T_1T_1$ " "
 2 $S_1S_3T_1T_1$ self-compatible
 or a ratio of 1 : 1.

Self-incompatible plants could be of the constitution $S_2S_3T_1T_2$ and would give a dihybrid ratio on selfing in the bud stage as in *Nicotiana*. Only four out of the sixteen possible matings of gametes would give self-compatible plants, i.e., two $S_2S_3T_1T_1$ and two $S_2S_3T_2T_2$ and the ratio obtained on selfing such a self-incompatible plant would be four compatibles to twelve incompatibles or 1 : 3.

This interesting hypothesis of Kakizaki merits further investigation. Lawrence (1930), however, points out that *Brassica* has basic numbers of 8, 9 and 10, and that the evidence from the number of chromosomes in the Cruciferae indicates that *Brassica* may be a secondary polyploid. We therefore suggest that Kakizaki's results may be the result of polysomic inheritance of incompatibility factors as Crane and Lawrence have already found in plums and apples.

Physiology of Pollen Tube Growth. That incompatibility is closely connected with pollen tube growth in the style, is supported by the histological studies of various workers. Jost (1907) finds that in *Lilium* the pollen tubes of self-incompatible plants grow so slowly that fertilisation is not achieved. Martin (1913) found that pollen tubes in self-pollinated red clover grew much more slowly than pollen tubes in a cross pollinated plant. Coe and Martin (1920), and Williams (1925) found that when red clover was pollinated in the bud stage it set more seed. Williams suggests that this fact may be correlated with the slow growth of its own pollen tubes. In the apple, Namikawa (1923) suggested that the "self" pollen tubes did not grow at a different rate from foreign pollen tubes, while Knight (1918) and Osterwalder (1910) were of a different opinion. Sansome (unpub.) studied the pollen tubes in Crane's apple material and found on style dissection that there was a great difference in growth rate in the style, between compatible and incompatible pollen. Namikawa in adopting transverse sectioning of the style and staining with iron-alum hæmatoxylin must have mistaken the stylar hairs for pollen tubes. Namikawa also thought that the pollen tubes descended outside the styles and entered the ovary at the base of the five styles in a similar fashion to those of the tulip. Sansome finds that the pollen tubes descend inside each style as in *Primula sinensis*. Other investigators, among whom are Correns (1913) for *Cardamine pratense*, Compton (1913) for *Reseda*, Moore (1917) for *Tradescantia*, Crane and Lawrence for cherries, plums and apples, East and Mangelsdorf for *Nicotiana*, Sirks for *Verbascum* and Gregor (unpub.) for *Lolium* and *Dactylis*, hold that the pollen tube growth in the style is the cause of compatibility or incompatibility of the matings in these plants.

Whether incompatible pollen tubes are inhibited in growth or whether compatible pollen is accelerated or whether both inhibition and acceleration may be present in these plants is as yet undecided. The success of pollination in the bud, of incompatible matings in *Nicotiana*, red clover and cabbage does not decide the matter since the development of inhibitory substances may be restricted to a certain period in stylar degeneration. End-season fertility, by which

normally self-sterile plants may give some seeds late in the season of growth, has been reported in *Nicotiana*, East (1923) and Anderson (1924), and in *Lythrum*, Stout (1922, 1923). It has been used by Kakizaki (1930) to support the view that there is an inhibitory action which wanes at the end of the season. This hypothesis, however, is open to the objection that the flower does not wither so quickly at that time, therefore the slower growing tubes achieve fertilisation owing to the time factor alone.

Evidence obtained by Kakizaki, Crane, and Lawrence, however, suggests that both inhibition of incompatible and acceleration of compatible pollen tubes takes place. In a tetraploid, although $S_1S_1S_2S_2$ styler tissue will not allow S_1S_1 pollen to fertilise the ovules, pollen tubes carrying S_1S_3 may be able to reach the ovules, due possibly to an acceleration of growth caused by the presence of S_3 . Here again there may be the objection that the ability of such a pollen tube to grow may be due simply to the nullification by S_3 of the inhibitory action of S_1 ; the production of some inhibitory substance normally induced by S_1 may be stopped at the source by the presence of S_3 , rather than as implied by Lawrence, to the production of both inhibitor and accelerator which interact with one another.

It should be mentioned, in passing, that the solution of the problem of incompatibility is of great importance to the fruit grower. It was well known, in an empirical manner, that certain fruit trees, if planted in isolation or in certain mixtures of varieties, were unproductive, and that certain other mixtures of varieties were productive. The scientific analysis has shown the cause of incompatibility and furnishes valuable information as to which trees will be compatible *inter se*.

All the above examples furnish evidence that the pollen grain carries genetic factors and that these genetic factors have been segregated one from another at the meiotic division which is undergone by the nucleus during the formation of the microspore from the microsporocyte.

Belling (1914) found that when he crossed two races of *Stizolobium*, 50% of the pollen and eggs aborted, and Brink (1929 b) found a similar behaviour in maize. A hypothesis was put forward that

there were two pairs of allelomorphs **Aa Bb** and that the gametes with the constitutions **AB** and **ab** were non-viable. Belling and Brink, however, make the important suggestion that some interchange or translocation in the chromosomes may account for these cases. Later we shall see that the latter explanation is substantiated by related facts.

Conclusions. Several definite conclusions may be drawn from the foregoing experiments. In the sporophyte, with a diploid constitution, factors controlling character inheritance are present in duplicate ; either there may be two identical allelomorphs, or in hybrids two different allelomorphs. These separate from one another at meiosis as self-propagating units uninfluenced by their association together. The resulting haploid generation contains one representative of each pair of allelomorphs. The genetic results from mosses, Fungi, ferns and pollen of Angiosperms indicate that segregation of the allelomorphs is definite and regular. The expectation of a $1 : 1$ ratio of segregation is found.

As postulated by Mendel, the gametes of a normal plant or animal are pure (but see p. 207) for one member of each pair of allelomorphs. Further, each pair of allelomorphs segregates independently of other pairs (but see p. 84). By random mating of the gametes produced in the definite $1 : 1$ ratio in respect of two allelomorphs, it is expected that the resulting zygotes will be formed in definite and corresponding proportions. Thus by selfing a plant which produces gametes containing factors **A** and **a** in the ratio $1 : 1$ we expect the progeny to be in the ratio of $(1A : 1a)^2$ or $1AA : 2Aa : 1aa$.

INCOMPLETE DOMINANCE

Some characters, such as distribution of colour in the flower of *Primula sinensis*, are not completely dominant. There are two factors **D** and **G** which suppress colour in the petals of *P. sinensis*. **G** makes the gynœcium green and inhibits the expression of colour in the centre of the petals. **D** inhibits colour on the periphery of the flower. Therefore a plant with the factors **DG** will have white flowers. In plants with red stigmas, *i.e.*, with the recessive factor **g** instead of the dominant **G**, it is found that these plants **DDgg** have

a coloured centre to the flower, the so-called "Duchess" type. **ddgg** flowers are pigmented throughout while **Ddgg** is flushed at the edges, the so-called "General Buller." Thus it is seen that plants of the constitutions **DD** and **Dd** are different in appearance, due to the fact that **D** is not completely dominant over **d**. If we cross two heterozygous plants **Ddgg** (General Buller) together, we obtain progeny in the ratio of 1 Duchess **DDgg** : 2 General Buller **Ddgg** : 1 fully pigmented plant **ddgg**.

INTERACTION OF FACTORS

Complementary Factors. It was thought by some of the early workers in genetics that the characters and factors were closely connected. The phrase "unit character," used instead of "factor," was adopted to indicate that for every heritable character exhibited by the plant there was an "id," "pangen" or unit which was transmitted through the gametes. This idea arose possibly under the influence of Weismann's idiomorph doctrine, that the germ plasma contained a factor for every detail of the plant which was inherited. It was soon realised that interaction between two or more factors had considerable effect on the characters of the plant. Thus Bateson and Punnett crossed two plants of "Emily Henderson," a white-flowered variety of sweet pea (*Lathyrus odoratus*) and obtained an F_1 , all of which had red flowers. On selfing this F_1 , the F_2 progeny segregated into nine coloured and seven white-flowered plants. It was found that two dominant factors **C** and **R** were required to be present together to produce colour, and when only one or neither was present no colour was produced. Hence the F_2 would segregate in the ratio $9CR : 3Cr : 3cR : 1cr$ (see checkerboard, Fig. 4), of which only the first group would be coloured. These factors **C** and **R** are called "complementary" factors.

It was found that another factor **B1** converted the red colour of **CR** plants into purple but did not affect the white flowered plants. An F_2 from the crossing of plants with the constitutions **CCrrB1B1** and **ccRRb1b1** (both white-flowered) segregated in the ratio of 27 purples : 9 reds : 28 whites. The factorial scheme can be summarised therefore as follows:—

CRB1 purple, **CRb1** red and other constitutions white.

The following examples are quoted to direct attention to the subject of complementary factors, a full account of which is given by Matsuura (1929) and Onslow (1925).

In *Matthiola incana*, Tschermak (1912) and Saunders (1928 b) found two complementary factors **C** and **R** for red sap colour. Other factors modified the expression of **C** and **R**. Two factors **H** and **K** were necessary for the production of hoariness, but these factors were only effective in the presence of **C** and **R**.

Blakeslee (1921 b) found that there were two different yellow bud cones in races of *Rudbeckia*, which, when intercrossed, gave a ratio of 9 purple : 7 yellow in the F_2 , indicating that two complementary factors were segregating. On treatment with potassium hydroxide, he found that one type of yellow turned black while another turned red. Hence by testing the F_2 progeny he separated the yellow group into a ratio of 4 which turned red to 3 which turned black. In other words, by chemical means, Blakeslee was able to identify those yellows which carried one of the complementary factors for purple.

In *Antirrhinum majus*, Baur (1910, 1911) found that ivory-flowered plants when crossed to certain white-flowered plants give a magenta F_1 and a ratio of 9 magenta : 3 ivory : 4 white in the F_2 .

Here, therefore, one of the dominant factors, even in the absence of the dominant member of the other pair, affects the character expression (ivory). Similarly, yellow-flowered \times certain white-flowered plants gives a red F_1 and a ratio of 9 red : 3 yellow : 4 white plants in the F_2 .

Onslow (1925, 1932) Wheldale (1910) and Wheldale and Bassett (1913, 1914) submitted the pigments of ivory, yellow, magenta and red flowers to chemical analysis. They identified the ivory and yellow pigments as flavones (glucosides of apigenin and luteolin). The yellow flower contains both flavones, but the ivory flower only contains glucoside of apigenin. The red and magenta flowers contain an amorphous anthocyanin pigment of uncertain constitution, as well as the flavones. Onslow (1925, 1932) pointed out that the relationship of flavones and anthocyanins was still an uncertain question. Scott-Moncrieff (1930) was able to identify the pigment in the magenta flowers as 3-rhamno-glucoside of cyanidin and points out that there is no connection by reduction or simple

oxidation processes between apigenin and cyanidin. Therefore the chromogen-enzyme hypotheses concerning the working of these complementary factors as put forward by the earlier workers must still remain unconfirmed. It is, however, significant that the **CR** type of inheritance of colour is widespread among plants and is probably connected with anthocyanin pigments in almost every case.

A somewhat similar position is found in *Dahlia variabilis*. Lawrence (1929, 1931 *a*) shows that there are four pigments, two flavones and two anthocyanins in the *Dahlia*. With the ivory flavone (apigenin) the anthocyanin colours range from ivory (no anthocyanin) to purple. With the yellow flavone the colours are yellow, orange or scarlet, with various intergrades. Schmid and Washkau (1928) identified a flavone in the yellow *Dahlia*, as apigenin, but Lawrence points out that the factor for ivory flavone is generally present as well as the factor for yellow flavone in yellow dahlias, therefore it is questionable as to which flavone the authors studied. The anthocyanins of the *Dahlia* are glucosides of pelargonidin and cyanidin. There are two separate factors **A** and **B** which cause the appearance of anthocyanin. **A** produces relatively pale pigmentation and **B** deep pigmentation. The evidence from *Dahlia*, however, rather indicates that the flavones and anthocyanins are independent, since anthocyanins can be formed without the presence of flavone (Lawrence unpub.). Nevertheless Lawrence's discovery (in press) that the amount of flavone is reduced when anthocyanin is formed appears to indicate a common source of material for manufacture. With ivory flavone **A** apparently forms cyanidin only. **B** with ivory produces mainly cyanidin, but pelargonidin may be present also. With yellow flavone **B** apparently produces pelargonidin only. Reference should be made to Onslow (1932) for later information on this subject.

That some factors influence the *pH* value of the cell sap of plants, and hence influence colour expression, is seen in varieties of *Papaver Rhoeas* (Newton, 1929), where such a factor converts the red petal colour to purple and in *Primula sinensis*, where the factor **R** makes the cell sap more acid (*pH* about 4) as compared with the allelomorph **r**, which gives a *pH* of 6 to the cell sap.

The following constitutions in terms of factors in *Primula sinensis* illustrate the colour reactions.

BBKKRR magenta,
 BBKKrr blue,
 BBkk (R or r) pale pink to white,
 bbkkRR coral,
 bbkkrr white,
 bbKKRR red,
 bbKKrr slaty blue.

The anthocyanins are indicators of acidity—the magenta anthocyanin produced by **B** is blue at pH 6 and therefore **BBKKrr** plants are blue, due to the factor **r**. The coral anthocyanin, produced under the influence of **K**, is colourless at pH 6, and therefore **bKrr** plants are white (de Winton and Haldane, unpublished).

In *Stizolobium* Belling (1914) found an interesting case. The velvet bean *S. deeringianum* has pods covered with black-brown tomentose hairs, together with a few long stiff hairs. The Lyons (*S. niveum*), Yokohama (*S. hassjoo*) and China beans have whitish, short downy hairs. The F_1 hybrids between the Florida velvet bean and the others have their pods covered with stinging bristles. The segregation indicates that three factors are involved. Stinging depends on the presence of the factors **B** and **C**. The factor **D** gives black hairs when **B** is absent, *i.e.*, the cross **BD** \times **bd** gives a ratio of 13 white : 3 black hairs in the F_2 . **B** is epistatic to **D** with regard to colour of hairs. Belling suggests that the Florida velvet bean possesses **C** but lacks **D** and **B**.

Complementary factors are involved in the production of glaucous leaves, Vilmorin (1911) and Wellensiek (1925 *a*, *b*), and of purple pods, Wellensiek (1925 *a*, *b*) and de Winton (unpub.) in *Pisum sativum*.

OTHER INTERACTIONS OF FACTORS (COMPLEMENTARY, EPISTATIC AND MODIFYING FACTORS)

In maize four factors **C, R, A, Pr** produce the full purple-coloured aleurone layer in the seed, East and Hayes (1911) and Emerson (1918).

The progeny of a plant heterozygous for three factors **C**, **R** and **A** segregates in a ratio of 27 coloured to 37 colourless, indicating that these three factors are complementary for colour. This phenomenon, where two or more non-allelomorphic factors affect the same character, is of frequent occurrence in plants and animals. One factor such as **Pr**, which converts the red colour of **CRA** into purple, may suppress the characteristic expression of these non-allelomorphic factors. Such a factor is epistatic to the hypostatic **CRA** factors (Bateson, 1930). One factor may modify without completely suppressing the expression of another factor. Such a factor is called a modifying factor. For example, Fraser (1924) found that the intensity of colour depended on a factor "**In**" the presence of which lightened the shade of colour produced by the factors **CRAPr** or **CRApr**. Hence the factors for aleurone colour are :—

CRAPrIn light purple,

CRAprIn light red,

CRAprin dark purple,

CRAprin dark red,

all other combinations being colourless.

East and Hayes have shown also that the presence of an inhibiting factor **I** prevents the formation of colour in the aleurone layer even when **CRAPr** are present. Emerson (1918) points out that the expression of colour in the aleurone grain layer is also influenced phenotypically by endosperm characters, which are controlled by factors independent of those mentioned. For example, with waxy endosperm the purple colour of **CRAPr** appears a dull black.

Kvakan (1924) added **Bn**, the factor for Brown aleurone to the factors involved in aleurone colour. When the endosperm is colourless, due to absence of **CRA**, the caryopsis is yellowish in the presence of **Bn**, but in the presence of **CRA** the aleurone assumes the brown characteristic. **Bn** is unrelated to the other factors in the development of colour in the aleurone. Thus **I** does not inhibit the expression of **Bn**.

The complex interaction of factors is further illustrated by colour inheritance in the vegetative parts of maize. Three fundamental factors are involved. **A**, the factor already seen in connection with aleurone colour, is necessary for the production of

anthocyanin. **P** converts the red of **A** plants to purple, and **B** gives rise to a flavone (brown). The scheme is therefore

ABP purple,
ABp sun-red,
AbP dilute purple,
Abp dilute sun-red,
abP brown,

all other combinations green.

Hence a cross, **ABP** × **abp** will produce in the F_2 a ratio of 27 purple : 9 sun-red : 9 dilute purple : 9 brown : 3 dilute sun-red : 7 green plants. Cf. Table 3 for the results obtained by Emerson (1921 b).

The backcross of the F_1 to the bottom recessive **abp** will segregate in the ratio of 1 : 1 : 1 : 1 : 1 : 3 of the above categories.

TABLE 3 (compiled from Emerson's results)

Cross.	Purple.	Sun-red.	Dil. purple.	Dil. sun-red.	Brown.	Green.	Total.
AaBbPp × AaBbPp	obs. 952	305	275	91	278	216	2,117
AaBbPp × AaBbPp	exp. 893	298	298	99	298	232	
AaBbPp × AaBbPp	obs. 170	160	176	160	172	479	1,317
aabbpp	exp. 165	165	165	165	165	495	

Dilute sun-red can be of two constitutions, **AA** or **Aa** with **b** and **p** in the recessive condition, and brown can be of four constitutions, **BBPp**, **BbPp**, **BbPp** or **BBPp**, together with the recessive **a**. The cross, dilute sun-red × brown will therefore give rise to a definite series of ratios, depending upon the constitutions of the parents used.

Emerson found that nine crosses of this type produced all purple offspring. The constitutions of the parents were therefore dilute sun-red **AAbbPp**, and brown **aaBBPp**.

Seven crosses of this type produced 143 purple (**AaBbPp**) and 147 sun-red (**AaBbPp**), therefore the parents were dilute sun-red **AAbbPp** and brown **aaBBPp**. Six crosses of this type gave 105 purple (**AaBbPp**) and 123 dilute purple (**AabbPp**). The

parents were therefore dilute sun-red (AAbbplpl) and brown (aaBbPIPl). Four crosses gave 9 purple : 11 sun-red : 19 dilute purple : 17 dilute sun-red, therefore the parents were of the constitution, dilute sun-red (AAbbplpl) and brown (aaBbPIPl).

It will be seen that although the phenotypes of the brown plants were alike, the genotypes were different and gave different products when crossed to dilute sun-red.

These results obtained by Emerson are extremely interesting and useful for the study of normal mendelian segregation of more than one factor. Emerson has tested out all the possibilities by intercrossing plants with the different constitutions, and has obtained confirmatory evidence of the correctness of this factor hypothesis.

In carrying out this work he was also able to show that there was a multiple allelomorph series, of which R , one of the factors concerned with aleurone colour inheritance, was one member. These allelomorph factors affect the expression of ABPl plants, and also several other combinations. For example, Rr and rr give pink anthers. Both are dominant to the allelomorphs Rg and rg , which give green anthers. Emerson found that plants which were normally dilute purple or dilute sun-red were green in presence of homozygous RgRg , but in the presence of Rr or rr they were normal.

The most remarkable feature of this allelomorph series is that a single factor behaves as a dominant to another of the series in respect of colour in one part of the plant, while in another part of the plant the same factor is recessive. Thus Emerson obtained the following results :—

Rrg gives green anthers and silks in all coloured plants except brown plants,

Rg and rg give green anthers and silks in purple and sun-red plants, and also give green plants in dilute sun-red and dilute purple plants,

Rch intensifies brownish purple and dilute purple probably through its action on the factor B ,

Rr is dominant for aleurone and plant colour,

rg is recessive for aleurone and plant colour,

rr and rch are recessive for aleurone colour and dominant for plant colour,

Rg is dominant for aleurone colour and recessive for plant colour, Rrg is dominant for both, but recessive for anther and silk colour.

In *Primula sinensis* there are at least seven main factors in the dominant condition which must be present to give the normal leaf shape (palmate) to the plant. The factors recessive to normal that have been identified by a characteristic expression of the leaf character are "fern," "tongue," "oak," "maple," "claw" and two different factors which crimp the leaf. (Gregory, de Winton and Bateson, 1923 and de Winton, unpub.). In *Pharbitis Nil*, Imai (1926-1931) finds that it is necessary for seven fundamental factors and three modifiers to be present as dominants, together with the recessive allelomorph of "Blown", in order that the normal leaf shape may be obtained. The recessives of the seven fundamental factors are "dragonfly," "cordate," "maple," "willow," "polymorphic," "acuminate," and "pear":—named according to the effect on the character of the leaf. Among these recessives it is found that dragonfly is hypostatic to both cordate and maple, and cannot be recognised in their presence. There is also a dragonfly suppressor which as a dominant inhibits the dragonfly recessive's action. Both in *Primula sinensis* and *Pharbitis Nil* these factors which have been identified by their effect on the leaf, influence the characters of other parts of the plant, and in particular the shape of the petals. For example, the willow factor in *Pharbitis* produces narrow cotyledons and petals and makes the plant female sterile, while maple divides the corolla into five cut segments in place of being gamopetalous. Obviously there will be many other factors in *Primula* and *Pharbitis* which control the development of the leaf.

Imai (1931 a, b) has summarised the known facts regarding flower colour in *Pharbitis Nil*. Besides three factors, W_1 , W_2 and W_3 , of which W_1 and W_2 are complementary for colour, the recessive factor pr, converts a blue into purple, and mg converts a blue into magenta, while prmg W_1W_2 is red. There is a factor dy which gives a dusky flower; this factor is hypostatic to dk, which gives a duskish flower. Governing flower tones, there is a factor, i, which intensifies colour, and two factors, lt_1 and lt_2 , hypostatic to i, which lighten colour. Dilute D is a dominant which reduces colour, while the factor for tinged is a recessive which also reduces colour intensity.

In *Pharbitis Nil*, Imai (1921) and Hagiwara (1923) (see Matsuura, 1929) found that the cross, red-stemmed white flower \times green-stemmed white flower gave a coloured F_1 and a ratio of nine coloured to seven white-flowered plants in the F_2 . Two complementary factors, **C** and **R**, are therefore concerned in colour production. In addition, three other factors, **A**, **Pl** and **B**, are concerned in modifying this colour, thus :—

CRAP**I**B blue.
 CRAP**i**b purple.
 CRA**p**lB purple.
 CRA**p**l**i**b scarlet.
 CRa**p**lB dark red.
 Cr, cR and cr combinations white.

In the neighbouring species, *Pharbitis purpurea*, Barker (1917) found two complementary factors, **C** and **R**, for colour production.

In *Portulaca grandiflora*, Yasui and Ikeno (cf. Matsuura, 1929) showed that five factors are involved in flower colour, thus :—

C orange,
 CG yellow,
 CF flesh colour,
 CR red,
 CRB magenta,
 c white.

Ikeno was able to identify phenotypically three types of white. White (1) is free from all pigment, and when crossed to orange gives in the F_2 , 3 orange : 1 white. White (2) has a few magenta spots on the petals or filaments, and when crossed to orange produces in the F_2 , 9 magenta : 3 orange : 4 white. Pseudo-white (3) has reddish pigment in the stem and leaves, and purple spots at the base of the white petals. Pseudo-white (Ps)**C** \times white (1) gives an orange F_1 and a ratio of 9 orange : 3 pseudo-white : 4 white in the F_2 . Pseudo-white is PsPs**CC**. The heterozygote Psps**CC** does not inhibit the orange of **C**. This is an interesting case of incomplete epistacy, and shows the effect of balance between factors on the character expression.

Tammes (1922, etc.) and Kappert (1925 a) found in *Linum usitatissimum* that three factors, $B_1B_2B_3$, were necessary for the production of the pink flower colour. Another factor, F, makes this pink colour deeper in shade, D converts the pink to lilac while the constitution $B_1B_2C_1DF$ is blue. An interesting fact is that some of the factors for flower colour in *Linum* affect other parts of the plant also. For example, blue anthers result from the interaction of a factor H and B_1B_2 D of the petal series. In the absence of any one of these four factors the anthers are yellow.

Seed coat colour is controlled by B_1D and a factor G. Tammes also suggests that B_1C_1 together, in the absence of D, cause a crinkled condition of the petals and have a semi-lethal effect. In *Linum angustifolium*, Tammes postulated a similar series of factors for flower colour, as in *L. usitatissimum*. The genetical behaviour seems to be similar, but the degree of expression of the factors is different.

This pleiotropic effect, by which one factor affects several character expressions, is also clearly demonstrated in *Lupinus* (Hallqvist, 1921), where a factor for red flower colour increases the height of a plant from 60 to 69 cm., and also induces the formation of anthocyanin in the vegetative parts of the plant. The same factor causes the seed coat to be glabrous and shiny, while the recessive factor causes a rough granulated seed coat. Hallqvist groups the pleiotropic effects of a factor into isophase and heterophase classes. In the isophase class the factor has a similar effect on several characters, while in the heterophase class the reactions are opposite in type.

Hallqvist (1921), Vestergaard (1921) and Sypniewski (1925), found four genes in *Lupinus angustifolius* which affect both flower and seed coat colour.

- R, a basic gene, alone gives red flowers and brown seed coat,
- RB gives blue flowers and greyish-brown seeds,
- RV gives violet flowers and rust-brown seeds,
- F is an intensifier of these colours.

Xenia. Xenia, or the direct observable effect of the genetic constitution of the pollen upon the young zygote, is reported in

Pisum sativum (round-wrinkled, yellow-green), Mendel (1865) *Lupinus*, *Vicia*, *Linum* and *Phaseolus vulgaris* \times *P. multiflorus* (colour of cotyledons) Tschermak (1930). The peculiar process by which endosperm is formed may allow the male parent to express its effect on the characteristics of the seed. Guignard (1901 *a, b*) and Nawaschin (1899) showed that the two nuclei of the embryo-sac fused together to form the central fusion nucleus, prior to fusion with the nucleus of the pollen grain. Weatherwax (1919) reinvestigated the process and showed that sometimes the nuclei did not fuse until the arrival of the pollen nucleus. Two nuclei are furnished by the pollen tube. One fuses with the ovum to form the new zygote, while the other fuses with the central fusion nucleus to form the endosperm. Where the endosperm is not absorbed into the embryo before germination (as in the so-called albuminous seeds), the characters of the endosperm may be analysed. In each cell of the endosperm there is one complement of chromosomes contributed by the male parent and two complements contributed by the female parent.

In accordance with this we find a definite type of factor interaction. For example, there are two races of maize, one with floury endosperm and one with flinty endosperm. When East and Hayes (1911) crossed these two races reciprocally they found that the endosperm of the seeds corresponded with that of the race to which the maternal parent belonged. The hybrid plants produced from the reciprocal crosses, however, were identical, and segregation in the F_2 was similar in both crosses.

If the flinty race carries a factor F and the floury race carries the allelomorph f , the results may be symbolised thus :—

flinty \times floury				floury \times flinty			
egg	endosperm	pollen		egg	endosperm	pollen	
F	FF	\times	f	f	ff	\times	F
embryo	endosperm			embryo	endosperm		
seeds Ff	FFf (flinty)			Ff	ffF (floury).		

It will be seen therefore that the embryos from both crosses are of the same constitution, but that the endosperms of the reciprocal crosses are of the constitutions FFf and ffF respectively. The dominance of F over f is insufficient to cause flintiness in the

presence of two doses of *f*. Similarly, the aleurone colour factor *R* is not sufficiently dominant over *r*. Endosperms of the constitution *rrR* (from the cross *rr* × *RR*) are mottled, while endosperms of the constitution *RRr* (from the reciprocal cross *RR* × *rr*) are fully coloured. *Xenia* has also been reported in rye (von Rümker, 1913). It is not, however, a general characteristic of the endosperm.

Usually, in endosperm, the dominant character is not suppressed by two doses of the recessive factor. For example, endosperm of the constitution *Susus* or *SuSusu* is starchy.

Nixon (1928) found that pollen from different varieties of the date-palm had different effects on the size of the fruit produced by one plant. Swingle (1928) suggested that the embryo and endosperm secreted a substance which influenced the development of the ovary (mother plant tissue). He proposed the term *metaxenia* for this effect of pollen upon the maternal tissue. Schaffner (1928) points out, however, that *xenia* is a definite effect of genetic factor balance, and that this supposed *metaxenia* is physiological in origin. He therefore prefers the term *ectogeny* in place of *metaxenia*. Nebel (1930) and Harrison (1931) have reported a similar phenomenon in apples and cotton respectively. Further investigation on this question seems desirable.

LETHAL FACTORS

Geneticists study mainly the behaviour of factors which are recognised by the presence of contrasting allelomorphous factors. They are able to study, for example, the inheritance of flower shape in *Primula sinensis*, but at present they are unable to study the factors causing the presence or absence of the flower itself.

Some factors such as crimp leaf (*f*) combined with the *sinensis* factor (*Ch*) have an abnormal effect on various plant characters of *Primula sinensis*. Others reduce the vigour of the plant considerably *e.g.*, "feeble minded," is a weak plant with stunted growth.

Throughout the life cycle a plant is dependent on the genetic material inherited from its parents. Where different allelomorphous factors are present within a species it is reasonable that there should be various degrees of vitality or viability of the genotypes. Hence the so-called lethal factors, which in general are recessive to the normal, can exert their influence at various stages in the life cycle.

Few lethal factors are known which affect gametic viability. Sub-lethal factors are known however, such as those isolated in *Nicotiana Tabacum deformis* (see p. 51), and, to a certain degree, the incompatibility factors. Gametic sterility, which is frequent among plants, is generally brought about by some chromosomal abnormality (cf. p. 254). Lethal factors affecting the gametes have been suggested in connection with the inheritance of doubleness in Stocks, but it is probable that the lethal is bound up with chromosome structure.

In Stocks, *Matthiola incana*, doubleness is recessive to the single-flowered form. Double flowers are completely sterile. Single-flowered plants may be homozygous for singleness SS , or heterozygous Ss , giving 3 singles : 1 double on selfing. Plants in another strain called "ever-sporting singles" or "d.races" are heterozygous, but on selfing give about 46-47 per cent. singles and 53-54 per cent. doubles. All singles of this strain behave in this manner. Saunders (1911, 1916, 1928 a, b) has also shown that only doubleness is transmitted by pollen of this race. Comparative tests on pollen germination of the above two races of singles have been made by Snow (1924, 1925) and Waddington (1929). Their results indicate that a factor is present in the ever-sporting single race which is lethal to pollen carrying it.

Linked with the factor S is a factor W for colourless plastids—the recessive w gives cream plastids.

A hypothesis has been put forward by Saunders which, although somewhat unorthodox, explains her results remarkably well. Hypotheses involving lethal factors have been advanced by Goldschmidt (1913), Frost (1915), Muller (1918) and Waddington (1929). Waddington adopts two gametic lethals l_w a pollen lethal, and l_s a pollen lethal and also an egg lethal only active when L_w is present (new terminology for these factors—after Frost, 1931). A pure

breeding single white is thus represented $\frac{L_s SL_w W}{L_s SL_w w}$, and an ever-sporting single sulphur white as $\frac{l_s Sl_w W}{L_s l_w w}$.

Crossing-over (see p. 84) is only supposed to occur between s and

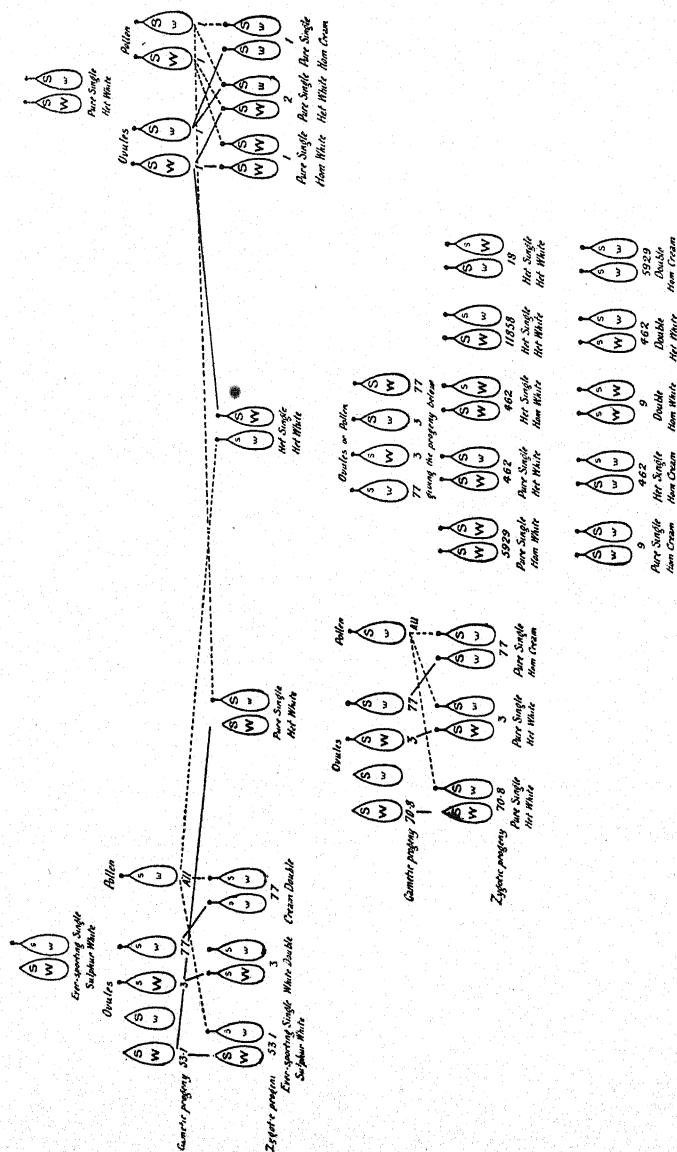


FIG. 6.—Diagrammatic explanation of the genetic behaviour of ever-sporting single, pure single and hybrid races of Stocks.

1_w . Philp and Huskins (1931) report that in the ever-sporting race, one of the chromosomes carrying the factors for singleness-doubleness (the *A* chromosome) lacks a trabant, 1. A pure

breeding single white is therefore represented by $\frac{LSW}{Lsw}$ and an ever-sporting sulphur white by $\frac{ISW}{Lsw}$. It is considered that 1 is lethal to

pollen containing it, and that on the male side, either 1 inhibits crossing over between the *A* chromosomes, or the cross-over gametes do not function. On the female side crossing over is supposed to take place between the region *S* and *W* and not between *S* and 1. 1 is incompletely lethal to eggs and a "Renner Effect" (see p. 277) is suggested.

Fig. 6, while showing the genetic behaviour of the various single-flowered races of Stocks on this hypothesis, also shows their general behaviour.

Saunders' results and the expected proportions on Saunders', Waddington's and the latter hypotheses are given in a table by Philp and Huskins (1931). Kvasnikov (1929) and Winge (1931) have found that occasionally the ever-sporting character is lost. This indicates that sometimes crossing over between *s* and the trabant *L* occurs, or, on Waddington's hypothesis, either double crossing over (see p. 112) between L_s and L_w occurs, or crossing over between 1_s and *S* and *S* and 1_w takes place in successive generations.

The young zygote of a plant has to survive under a number of environmental conditions not met with in the rest of the life cycle. The formation of endosperm, the assimilation of the storage products and germination are critical functions which have to be undertaken by the young zygote. The fact that geneticists find genotypes which fail in these respects and are able to study their inheritance is an answer to the objection of some biologists that the science of genetics only embodies a study of less vital characters such as colour, size and shape. Strangely enough some other biologists consider that genetics only involves the study of lethal characters.

Mangelsdorf (1926) and Jones (1920) found seeds of maize with defective endosperm, a character which behaved as a simple

recessive to the normally developed endosperm, while Lindstrom (1923) described abortive "flint defective" and "sweet defective" seeds. Demerec (1923) reported "germless" and Eyster (1922) added "scarred," while Wentz (1924) and Garber and Wade (1924) found other types of aberrant development of the seed.

TABLE 4

The Percentage of Germination in Defective Seeds of Fourteen Stocks Compared to the Theoretical Germination of Normal Seeds of the Same Relative Development (Mangelsdorf 1926)

Stock.	Defectives.	Theoretical Normal.
de_1	45.6	91.0
de_2	44.9	94.0
de_3	54.0	66.5
de_4	3.5	75.5
de_5	11.2	47.5
de_6	11.8	72.5
de_7	19.6	49.0
de_8	0	42.0
de_9	0	17.0
de_{10}	0	39.0
de_{11}	0.8	22.0
de_{12}	0	10.0
de_{13}	0	12.5
de_{14}	0	3.5

All are genetically controlled by factors which are recessive to normal.

The seeds having defective endosperm exhibit a range in the degree of abnormality. Mangelsdorf isolated fourteen different factors all recessive to normal which gave seeds with a greater or less development of endosperm. The endosperm of these seeds differs from normal endosperm more in quantity than in quality. In no case does defective endosperm attain the size of normal endosperm.

The fourteen factors controlling the character may be arranged

in order in proportion to their effect. de_1 gives an endosperm which is half the size of normal and there is a range to de_{12} and de_{14}

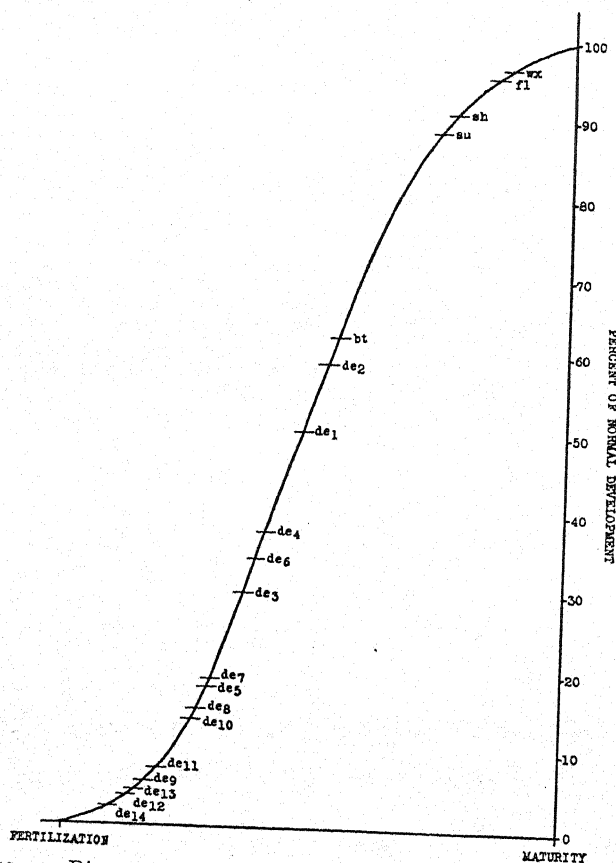


FIG. 7.—Diagram in which the relative development of endosperm characters is represented by points on the growth curve of normal seeds of maize.

where only a small fraction of endosperm is found. In all cases the endosperm begins development as in a normal seed, but differences soon appear in the rate of growth of normal and defective seeds. When the factor de_4 is present the embryo is formed, but it

disappears apparently by absorption at the same time as the endosperm. The relative stage of development of the endosperm of these fourteen types of seeds at maturity is shown in Table 4.

Any one of these fourteen factors causes one-quarter of the seeds on the ear of a heterozygous plant to be defective. There is also another factor de_{pi} which causes all the seeds in one quarter of the progeny to have defective endosperm. Thus de_i — de_{i4} affect the tissues of the zygote early in life, while de_{pi} is a so-called "plant" factor which affects the sporophyte in such a way that all the seeds produced are abnormal. Mangelsdorf also reports a factor "brittle" which, in expression of texture of endosperm, is intermediate between sugary and "shrunkened," and points out that the five characters—waxy, floury, shrunkened, sugary and brittle—and the fourteen defective endosperm types can be arranged in order of percentage of endosperm development. The accompanying graph (Fig. 7), is taken from Mangelsdorf (1926). To attain normal seed development, maize must therefore have at least eighteen dominant factors, any one of which in the homozygous recessive condition would reduce endosperm development to a greater or less extent.

This interesting case has another significant feature. The development of endosperm under the influence of factors which do not differ greatly from normal, passes through the stages finally reached by endosperms under the influence of factors lower in the scale. The S shape of the graph is similar to a growth curve and this correspondence may be significant. The expression of some of the factors is qualitatively different (e.g., "waxy," "sugary"), as well as quantitatively different. Linkage studies (see Table of Linkages) show that the various factors are carried on different chromosomes and are not allelomorphic. We cannot say, however, whether the factors themselves have any phylogenetic connection.

Mangelsdorf (1923, 1926), Lindstrom (1923) and Eyster (1924 b, c) describe recessive factors in maize called "primitive sporophyte" by Eyster and "premature germination" by Mangelsdorf. These factors, of which nine or perhaps ten are known, ge_i — ge_{10} (Mangelsdorf), pm_i — pm_2 (of Eyster), cause the seed to germinate without undergoing a resting period. ge_1 , ge_2 , ge_3 , ge_4 and ge_5 are

five independent recessive factors each of which causes premature germination, ge_6 and ge_7 are independent duplicate factors, both being necessary in the recessive condition to give premature germination, while ge_8 and ge_9 are linked duplicate factors. By sectioning the seeds it was found that in seeds containing the premature germination factors, the production of enzymes by the scutellum (to break down the storage materials of the endosperm) began at a very early stage. The resting stage is thus cut out. Although the stocks were known to contain the factors for green seedlings and yellow endosperm, the presence of ge_1 , ge_3 or ge_5 in the homozygous recessive condition gave white seedlings and white endosperm. The stock with ge_1 , which germinated slightly later than the other two, sometimes had a green tinge in the cotyledon. The other factors which had a less intensive effect on the induction of germination gave green seedlings and yellow endosperm. If the factor for premature germination causes enzymes for the breakdown of storage material in the endosperm to act too soon, it will interfere with the action of other factors controlling endosperm or embryo characters.

Oppenheimer (1922) has found that seeds of tomato, gourd, cucumber and *Nicotiana rustica* can be prevented from germinating by surrounding them with crushed tissue of the ovaries of the mother plant or by placing them on filter paper saturated with extract of this tissue. The degree of suppression is approximately proportional to the amount of tissue present or to the concentration of the extract. This effect can be overcome by heating the extract to 100°C . It is suggested that volatile substances may be produced by the mother plant which inhibit germination.

Mangelsdorf found that immature normal seed of maize attached to an ear, when enclosed in a damp cloth, absorbed water but did not germinate. Moistened seeds, from the same ear, placed in an ordinary germinator, germinated in a fortnight, which is a much longer time than dried immature seeds would take. The factors for premature germination may determine the non-production of such an inhibiting substance. From the foregoing it follows that at least twenty-seven dominant factors must be present for the normal development of maize seeds.

The onset of sexual maturity may bring to light some factor which has a lethal effect. A factor such as "bootlace" in tomato causes a deformity of the leaves and of the habit of the plant and assumes importance at gametogenesis by giving abnormal flowers. Honing (1923) describes an interesting case of sub-lethality in *Nicotiana* which illustrates how the growth reaction of a plant of a given genetic constitution varies with the environment.

He found an aberrant form of Deli tobacco in Sumatra cultures which is known as *deformis*. In Sumatra it was characterised by short internodes, deformed leaves and no flowers. It behaved as an incomplete recessive to the normal form and frequently died. Honing brought the stock to Holland and found that this *deformis* grew to twice the size of Sumatra *deformis* and produced fertile flowers. The characteristics were not so extreme in Holland as they were in Sumatra. Honing suggests that there is a single factor difference between *deformis* and normal Deli tobacco and that this factor controls enzyme action, as had been suggested by Goldschmidt (1916), Beyerinck (1917), etc. The reaction of *deformis* and normal tobacco to the different environments certainly supports this view. In the warm conditions of an early season in Holland, Deli flowers before *deformis*, but in a cold season *deformis* flowers first. In the F_1 hybrid between the two types the characteristic leaf deformation does not occur before the eleventh or twelfth node, whereas in the recessive form it is found as soon as the third or fourth node. In both cases the deformation increases in intensity with the ascent of the stem. Honing suggests that the *deformis* plants exhibit greater deformity on account of the earlier start and the greater rate of the enzyme action during development, as compared with the other types.

Whether or not one accepts the hypothesis of the enzyme nature of factor action, it seems probable that the effect of this factor is only sub-lethal because it is interfering with the processes of development occurring normally under Sumatra conditions and possibly such a factor would not be lethal in sub-arctic conditions. *Nicotiana* would not survive under sub-arctic conditions, however, since other factors are present which, under tropical conditions, are either active or passive in the normal mechanism of development.

BALANCED LETHAL FACTORS

If two lethal factors are in one linkage group the condition of balanced lethal factors may be present. Phipps (1929), for example, showed that virescent-8, a lethal virescent recessive of maize, was strongly linked with the factor for tunicate ear which produced sterility when in the homozygous dominant condition. If a plant

of the constitution $\frac{v_8tu}{V_8Tu}$ is selfed it will produce three types of viable zygotes—homozygous dominants, heterozygotes, and homozygous recessives. The recessives will die in the seedling stage on account of the lethality of v_8 , while the dominants will be sterile through the sterility of tunicate.

This race of maize, therefore, perpetuates itself only by the heterozygote which is a "balanced heterozygote." A cross-over between v_8tu and V_8Tu , which occurs once in 451 individuals, will give rise to gametes v_8Tu and V_8tu , and the latter type on fusing with a similar type will give a normal homozygote.

Baur (1924) had shown that the aurea variety of *Antirrhinum majus* only existed in the heterozygous condition and on selfing gave 2 aurea : 1 green : 1 non-viable homozygote. He also described a recessive lethal white type. When both aurea and alba were segregating in the same progeny, the ratios obtained were shown by Gairdner and Haldane (1929) to agree with the hypothesis that the factors controlling alba and aurea were linked, the cross-over percentage being about 10%. The double heterozygote

$\frac{\text{alba} +}{+ \text{aurea}}$ *, in which it will be noticed that the recessives are repulsed,

gave 9.5 yellows : 1 green together with inviable plants. The heterozygote therefore breeds nearly true, as one would expect.

In these two examples the characters which cause the lethality can be recognised and the balanced lethal conditions may be traced. The two factors in maize were closely linked, but the expression of each appeared at different points in the life cycle. In the *Antir-*

* The + sign beside alba represents the normal allelomorph of aurea and similarly the + sign beside aurea represents the normal allelomorph of alba.

rhinum case the linkage was not so close, and thus the balanced lethal system broke down more frequently and gave normal green plants.

More usually the factors which are acting in a balanced heterozygote affect the embryo in such a way that one is unable to study the mode of zygote elimination. Nevertheless, the genetic data are often sufficient to show that a balanced lethal mechanism is present. The phenomenon has been studied in various organisms such as *Drosophila*, *Plantago* and *Matthiola*, but it has assumed great evolutionary importance in the balanced heterozygotes of *Aenothera*. Here the self-perpetuation of a species such as *O. Lamarckiana*, which is genetically and cytologically a structural hybrid, depends upon such a mechanism of balanced lethals or upon one closely analogous to it.

The balanced lethal system enables a heterozygote to be self-perpetuating. The closer the lethals are linked the more efficient the system becomes. Beaded wing in *Drosophila* (Muller, 1917, 1918) is a dominant lethal. While attempts were being made to obtain a stock which was pure for the character Beaded wing, a pure breeding stock appeared suddenly, but it was, however, of the constitution Bd/+. The reason for this Beaded wing heterozygote breeding true was the appearance of another lethal closely linked to Beaded wing but on the homologous chromosome, *i.e.*, a balanced lethal system had been set up. Muller points out that if a certain heterozygote is selected by nature, or artificially as in the case of Beaded wing, a lethal will appear sooner or later, by mutation in the required position, to form a balanced lethal system. The frequency of the rate of mutation is high enough in *Drosophila* to make the chance appearance of a lethal in the required position reasonably possible.

VARIEGATION

Among plants, variegation is of widespread occurrence. Either the vegetative parts exhibit an irregular mosaic as in *Abutilon Thomsoni* and *Aucuba japonica*, or there is a regular arrangement of stripes or sections of chlorotic tissue between the normal green, or there is a general chlorosis over a larger or smaller portion of the plant.

The mosaic form is often transmitted by a so-called virus from one plant to another. Examples are *Aucuba japonica*, "breaking" in *Tulipa* (Cayley, 1928, Hughes, 1930), mosaic in tobacco, potato and other *Solanaceae* (see "Handb. Pflanzen Anatomie sect. Zelle und Cytoplasma" 1927, and Barton-Wright (1932), for a general account of this phenomenon).

With the above exceptions transmission of variegation from parent to offspring may take place, either by means of nuclear factors or by extra-nuclear means such as the plastids or cytoplasm. Biparental inheritance is found in *Antirrhinum*, *Melandrium*, *Pelargonium albomarginata*, Baur (1910), *Hordeum*, Nilsson-Ehle (1913), *Urtica pilulifera*, *Mirabilis Jalapa variegata*, Correns (1909 a, 1910, 1913, 1915, 1919), *Aquilegia*, *Lunaria biennis*, *Capsicum*, Ikeno (1917), *Barbarea vulgaris*, Dahlgren (1921), Andersson-Kottö (1923), *Zea*, Emerson (1912), Phipps, Demerec *et al.*, among many other plants.

Inheritance through the mother plant only, takes place in *Humulus*, *Primula sinensis*, *Zea*, *Pelargonium vars.*, *Melandrium vars.*, *Mirabilis Jalapa albomaculata*, *Arabis*, *Aubretia*, etc.

Maternal Inheritance. In the latter type of inheritance one may be reasonably sure that plastids instead of nuclear factors act as the carriers of the chlorotic condition. Gregory (1915) suggested that the transmission of diseased plastids through the egg and not through the pollen in *Primula sinensis*, would account for the maternal inheritance of the chlorotic form that he observed. He found diseased plastids in the cells of chlorotic tissue in these plants.

Green, white and variegated green and white plants are found in *Melandrium*. The pollen parent does not influence the variegation of the offspring in the above-mentioned plants and it is found that if the egg arises from sub-epidermal tissue, which is genetically green, the progeny will be green. If it arises from white tissue the progeny will be white, and if it arises from a variegated sub-epidermis the degree of variegation of the progeny depends on the degree exhibited by the particular portion of the sub-epidermis involved.

The cytoplasm and plastids enter the egg from the mother plant,

but it is of some importance to know whether any cytoplasm and plastids or their primordia enter the egg from the pollen tube.

Correns (1909 *a*) made the suggestion that no chloroplasts or cytoplasm of male origin were introduced into the egg, and that the transmission of variegation from mother to offspring in *Mirabilis jalapa albomaculata* was dependent on the cytoplasm or plastids derived from the mother. The question arises as to whether the plastids or some physiological condition of the cytoplasm is the causal agent for white or green plastids. In *Taraxacum*, *Senecio* and *Mirabilis* the demarcation between normal and chlorotic tissue is well defined. Correns points out that the intermediate zone between two areas is expected to be large when the plastids are mixed in type and are distributed at random to the daughter cells. The cell descendants from an embryonic cell containing a mixture of plastids (white and green) would have a greater chance of containing a mixture than of containing either all white or all green plastids. Correns (1922 *a*) comes to the conclusion,

“Bei den echten albomaculatae besteht bis zu einem gewissen embryonalen Zustand des Gewebes (der bunten Pflanze oder eines bunten Astes) noch in jeder Zelle die Möglichkeit, sich entweder normal zu entwickeln und grüne Chromatophoren zu bilden oder krank zu werden und dann blasse Plastiden zu haben. Die gleiche Möglichkeit müssen wir auch für das embryonale Gewebe bei einer albomarmorata oder einer anderen mendelnden weissbunten Sippe annehmen. Bei einer solchen ist das Verhalten aber durch ein Gen bedingt, bei einer albomaculata handelt es sich um einen (wohl schon krankhaften) Zustand der Zelle. Die Umwandlung dieses ‘primären’—homogenen, nicht mosaikartigen—Zustandes in den gesunden oder den definitiv kranken erfolgt bald früher, bald später, meist so früh, dass sich auch nach dem Eintritt des definitiven die Zellen noch teilen. Die Bestimmung ist nicht umkehrbar und erfolgt nicht durch irgendwelche inäquale Zellteilungen. Zwischen den gesunden und kranken Bezirken können Zonen lange im indifferenten Zustand verharren; schliesslich sind, wenigstens bei *Mirabilis* und *Primula*, alle (oder fast alle) Zellen in den einen oder anderen definitiven Zustand übergeführt, so dass dann das

fertige Gewebe, wenigstens gewöhnlich, nur mehr aus wirklich gesunden und wirklich kranken Zellen besteht."

This assumption suggests that the plasma influences the development of the plastids in a similar way to the effect of nuclear factors.

TABLE 5
Chlorophyll Deficiencies in Maize (Phipps, 1929)

Character.	Number of factors concerned.
White seedlings, w_1 to w_{11}	11
Dominant white seedlings	1
Xantha seedlings, xn_1, xn_2	2
Pale green seedlings, pg_1 to pg_5	5
Yellow-green seedlings, yg	2
Virescent seedlings, v_1 to v_{20}	20
Yellow-white seedlings m_1, m_2	2
Ghost seedlings, gh	1
Golden, g_1, g_2	2
White-base leaf, wl	1
Argentia, ar	1
Fine-striped, f_1, f_2	2
Fine-streaked, fi	1
Lineate, li	2
Japonica-striped, j	1
Green-striped, gs	1
Maternally inherited striping	—
Ioijap striping	1
Zebra-striped leaves, zb_1, zb_2	2
White sheath	1
Piebald seedlings, pb_1 to pb_4	4
Polka-dot leaves, pk	1
Blotch leaf, bl	1

65

For references to the various workers, see Phipps, 1929.

Bi-parental Inheritance. Bi-parental inheritance of variegation may be controlled either by nuclear factors or by the cytoplasm or plastids. Inheritance of variegation governed by nuclear factors is found in *Antirrhinum*, Baur (1910), Chittenden (1927 a), Gairdner and Haldane (1929), *Urtica peraurea*, *Mirabilis jalapa variegata*, Correns (1920, etc.), *Pelargonium chlorina*, *Zea*, and other species.

Usually green is completely dominant over the non-green form,

but sometimes, as in *Urtica*, *Pelargonium*, *Antirrhinum* and maize, the F_1 plants between green and non-green are variegated. When *Urtica peraurea*, which exists only in the heterozygous state, is selfed, the progeny segregate in the proportion of one white which dies, two peraurea and one green.

The variegated form of *Mirabilis Jalapa* is completely recessive to the normal form and the F_2 segregates in the proportion, three normal and one variegated. The F_2 ratios are not, however, constant. This is probably due to the inconstancy of the variegated form which often sports green branches.

In maize, Emerson (1912), Lindstrom (1918, 1921, 1924, 1925) and Phipps (1929), describe a large number of factors connected with variegation which exhibit peculiar interactions and a variety of expressions.

There are at least sixteen factors, any one of which in the homozygous recessive condition gives virescent seedlings and eleven of which give white seedlings which later may become green.

The various virescent seedlings (Demerec, 1924 *b*, and Phipps, 1929) may be arranged in a series ranging from white seedlings, which develop a small quantity of chlorophyll at ordinary temperatures, to seedlings which are white at low temperatures only and green at normal temperatures, v_5 . Cf. Table 5.

The interactions of these factors are of great interest. For example, the three factor pairs W_1w_1 , W_2w_2 and W_3w_3 , are inherited independently, and the dominants are complementary for normal green colour. On selfing a triple heterozygote, numbers approximating to the ratio 27 green : 37 white seedlings were obtained in the progeny. The factors W_5 and W_6 are linked and both must be homozygous recessive to give a white seedling. w_8 and w_9 are another pair of duplicate factors for white. Demerec (1923).

The authors Lindstrom, Emerson *et al.* have shown that a normal green plant must contain the dominant allelomorphs of all these factors for albinism, together with dominant allelomorphs to a series of virescent factors (v). If one of the virescent factors is in the recessive condition another set of factors L_1L_2 for yellow colour may be observed.

The factor scheme is :—

LVW, IVW, green,
 L_vW, virescent,
 l_vW, IVw, l_vw, yellow,
 LVw, white.

The green plants can therefore be of two types. One, IVW, when crossed to a white, will segregate for yellow pigment in the F₂, while the other, LVW, will not. Lindstrom (1925) found that the factors L₁ and L₂ react with the factors W₁W₂W₃ in different ways. l₁W × L₁w₁ gives in the F₂ a ratio of 12 : 3 : 1, while l₂W × L₂w gives a 9 : 3 : 4 ratio. In the first case the plant of the constitution l₁W is green instead of yellow—the factor W inhibits the action of the yellowing factor.

Two virescents when crossed together segregate in a 9 : 7 ratio. Only four combinations of the eighteen factors for virescent seedlings were not tested by Phipps.

In addition to the above there are other factors in maize which determine green striping on the leaf—japonica striping St, green, yellow and pale yellow stripes Lj, and white striped japonica lj, as well as the fine striped leaf caused by ff.

Plastid Inheritance. Baur's work with *Pelargonium albo-marginata* shows that instead of the vegetative parts being irregularly marked with white as in *Mirabilis*, the *Pelargonium* is a periclinal chimæra of white over green. We know that the epidermis of both white and green tissue appear the same and that the sub-epidermis will have normal green plastids in a green portion and abnormal plastids in a white region, *i.e.*, the chimærical nature is observable. The gametes are formed from the sub-epidermis. Baur crossed green plants with white over green chimæras reciprocally and found that the resulting seedlings consisted of greens, whites which died, and green and white chimærical plants. There was a quantitative difference between the reciprocal crosses.

	Pure green.	Green white.	White.
Green × green white periclinal chimæra	139	18	4
Green white × green	60	23	0

Thus when the chimæra was used as female, more mosaics were found in the progeny than in the reciprocal cross. The gametes of the chimæras were from white tissue in these crosses. Baur favoured the view that the inheritance was not chromosomal but was by plastids which had been transmitted by both gametes along with the nucleus from the pollen tube as well as from the egg. Noack (1922), Chittenden (1927 *a*) and Baur by inter-crossing green, white and the bi-parentally inherited aurea forms of *Pelargonium* showed that the white type carried the dominant allelomorph to aurea.

Ikeno (1917 *a, b*) found that reciprocal crosses between green and variegated types of *Capsicum annuum* gave only variegated progeny. Indeed, Ikeno found that green branches of a variegated plant gave variegated progeny and suggested that the cells of this branch contained some diseased plastids. He also suggested that since the inheritance was bi-parental and since intensity of variegation was correlated with the degrees of variegation of parent and offspring, the pollen carried over plastids and plastid primordia to the egg. Winge (1917) showed that only variegated progeny came from variegated plants in *Humulus* with transmission only through the female side.

Kondo, So and Takezaki (Imai, 1928) find that variegated barley seedlings are recessive in condition to normal. The variegation is not a definite character, but depends on the proportion of white plastids present. Albino seedlings are only found when the mother plant is variegated. Imai commenting on these experiments points out that if G causes green and if its recessive allelomorph G_1 causes variegation, there is apparently a mutation of green plastids to white in the presence of G_1G_1 , since the plastids were originally normal. These white plastids in variegated plants give rise to the maternal transmission of albinism. In presence of G_1 , normal plastids may change to white in the early somatic divisions, but not at gametogenesis or in the later somatic stage. The cross, variegated \times green male gives a green F_1 together with a few albinotics which are lethal. The F_2 segregates into 3 green : 1 variegated. White spikelets produce the same result as green spikelets on a variegated plant. It would seem therefore that G has the power of restoring

a proportion of white plastids to their normal green condition in the F_1 of the cross. This curious case requires further investigation.

Discussion. Baur (1930) accepts Correns' view that the cytoplasm of the *albomaculata* forms such as in *Mirabilis* may be the bearer of something which influences plastid behaviour. Baur, however, upholds his own view expressed in 1909, that in such forms as the bi-parentally inherited *albomarginata Pelargonium*, inheritance of variegation depends on the plastids themselves. This is also the view taken by the investigators of *Primula sinensis*, Gregory; *Capsicum*, Ikeno; and E. G. Anderson, who has investigated a maternally inherited variegation in maize.

Both Baur and Winge suggest that those cases in which the variegated type is of a general chlorotic type, may result from a diseased cytoplasm, but where definite chimaerical structure is observable the inheritance may be by plastids. Winge also suggests that the maternal inheritance of plastids as in *Primula sinensis*, and bi-parental inheritance in *Capsicum* and *Pelargonium* may be due in the latter case to transmission of plastid or plastid primordia by the pollen tube, whereas in the former case no such type of transmission takes place.

The mode of inheritance of variegation may be classified thus :—

- (1) Inheritance through the egg, resulting in yellow seedlings, *e.g.*, *Humulus*, probably cytoplasmic in origin.
- (2) Inheritance through the egg, resulting in white, variegated and green seedlings, *e.g.*, *Melandrium album*, probably plastid in origin.
- (3) Bi-parental inheritance, giving variegated seedlings, *e.g.*, *Capsicum*, probably cytoplasmic in origin.
- (4) Bi-parental inheritance, giving white, green and variegated seedlings, *e.g.*, *Pelargonium*, probably plastid in origin.
- (5) Bi-parental inheritance, giving both 1 chlorotic and 2 variegated and 3 white, green and variegated forms, *e.g.*, Maize, *Antirrhinum* (*aurea* and *alba*), nuclear in origin.

Variegation in Ferns. Andersson-Kottö (1923, 1930, 1931) has made some important contributions to the inheritance of variegation in ferns. Variegated sporophytes of *Lastræa atrata* are composed of two tissues, green and white, due to their contents of green and white

chloroplasts respectively. The gametophytes from both green and white sporophytic tissue are green, but the succeeding generation of sporophytes is all variegated. The plants are apogamous and both sporophyte and gametophyte have the same chromosome number. Obviously variegation appearing in the sporophyte and not in the gametophyte must be influenced by a time factor.

In *Scolopendrium vulgare* both gametophyte and sporophyte can show chlorophyll deficiency. Parts deficient in chlorophyll are golden yellow or pale green, and are called "pale" for convenience. No effect of environmental influence is apparent.

It was to be expected that a spore from a pale area would produce a pale gametophyte, but this was not always the case. Since a sporangium arises from one cell in the Leptosporangiate ferns, and since only green or pale gametophytes arise from any one sporangium, it is probable that when green gametophytes arise from pale areas of a sporophyte, the change from pale to green in a pale area must have occurred at the formation of the archesporium.

Green gametophytes do not mutate to pale but the variegated sporophytes, even those arising from selfed pale gametophytes (hence homozygous) may mutate in either direction. Sporophytes arising from a selfed green gametophyte are on the other hand always stable, green, and give green gametophytes in turn.

The data are adequate to show that the plastids themselves are not the means of transmission. Factors in the nucleus, in the cytoplasm or a definite condition of both nucleus and cytoplasm may later be found to be the cause of this peculiar behaviour. Mutation certainly takes place during the cell division of the sporophyte.

In *Polystichum angulare* the behaviour is still more complicated. The change from white to green or the reverse may take place early or late in the ontogeny of the sporophyte.

The gametophytes can be of four types. (1) green, (2) white, called p, which die in the 4-5-cell stage, (3) variegated prothalli, which always start as d cells, after which p cells are laid down by the growing point. Later, d cells may again be laid down by the growing point. The meristematic cells of a gametophyte may therefore mutate to pale and then back to green.

The p and d cells are phenotypically and genetically dissimilar, although in the presumably haploid state of the plant.

(4) The fourth type of gametophyte is pseudo-variegated. It is similar to the previous type until the 15-50-cell stage, when the p cells undergo an "after-greening" process so that in the mature stage the prothalli cannot be distinguished from normal. The genetics of the gametophytic generation show a surprising condition in which there is a complicated but obviously orderly process of mutation of one factor from one state to another. The following quotation from Andersson Kottö (1931) summarises the facts and suggests a descriptive hypothesis of different states of the one factor.

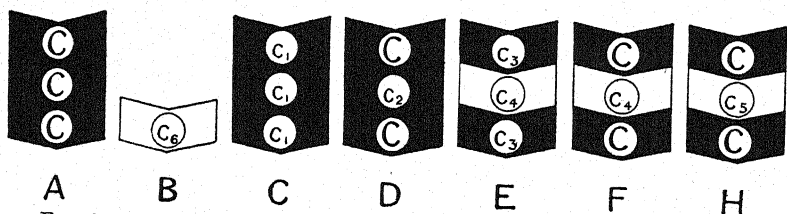


FIG. 8. Showing types of gametophytes from variegated sporophytes of *Polystichum angulare*. A, C and D are green (d); B is pale (p); E and F are variegated (var. IV); H is variegated (var. III.). The different types of gametophytes are regarded as containing a factor in seven different states C, C_1-C_6 , the factor in each state being stable or unstable and having its own characteristic mode of activity. C, C_1-C_6 indicates the genotype of different parts of these gametophytes.

"The changes (mutations) from green to pale in different cells are due to changes in a factor determining chlorophyll development, this factor being assumed to exist in seven different states. The factor in each state is either stable or unstable. The instability consists in change (mutation) from one state to another at various stages of the life cycle, the factor in each state having its characteristic mode of activity. The different states of the factor are designated $C, C_1, C_2, C_3, C_4, C_5$ and C_6 . Of these C is stable for green; C_6 is pale, (p, non-viable).

Appearance of the gametophytes (see scheme 1) :

C, C_1 and C_2 are green (d).

C_3 and C_4 are variegated (var. IV).

C_5 is variegated (var. III).

C_6 is pale (p) non-viable, gives no gametes.

Appearance of the sporophytes :

CC, Cc₁, Cc₂, Cc₃, Cc₄, c₁c₁, c₂c₂, c₃c₃, c₄c₄, and c₂c₃ have been ascertained to be green. All the combinations with c₅ are probably variegated, but test combinations were made only of c₅ × C (from different types). All other combinations are probably green.

The states of the factor in the gametophyte (see scheme I) :

C is stable

c₁ is stable

c₂ is unstable and gives cells with c₂ and other cells with C

c₃ " " " " " " c₄ " " " " c₃

c₄ " " " " " " c₄ " " " " C

c₅ " " " " " " c₅ " " " " C

c₆ is stable but perishes without giving gametes (p).

States of the factor in the sporophyte :

C is stable

c₁ gives c₁ + c₆ + C

c₂ " c₃ + c₄

c₃ " c₃ + c₄

c₄ " c₄ + c₃ + c₆

c₅ " c₅ + c₁ + c₂ + c₄ + c₆ + C).

To account for the location of the mutation in the growing point of the variegated gametophyte and for the genotypical constitution of the different parts of the var. III gametophyte and particularly for the fact that though the mutation capacity must be 'present' in the somatic cells of the basal green part (C) of the var. III gametophyte, since p cells are developed from it, it is 'absent' in the gametes and progeny derived from this same green part of the gametophyte, it is assumed that *the reduced spore contains the factor in the c₅ state. At each division the factor in this state is in a labile or unstable primary condition with the potentiality of C and c₅, i.e. the two states found in this gametophyte, and two possibilities exist : (a) the formation of stable green and (b) the retention of the unstable c₅ state.* It is assumed that c₂ and c₄ behave in a similar way, the c₃ mutating from one unstable state to another. Each state remains at many successive divisions of the growing point. The c₁ remains in the same state throughout the gametophyte" (Andersson-Kottö, 1931, pp. 291-292).

The investigation indicates a strong possibility that periodic mutations like those described for *Polystichum* are due to periodic alterations in the structure of the gene other than loss or gain of parts.

The influence of the contents of the cytoplasm on the transmission of variegation is therefore indicated in several cases and proved in others. The cytoplasm may also affect the expression of the characters determined by nuclear factors.

CYTOPLASMIC INFLUENCE ON THE EFFECT OF NUCLEAR FACTORS

Several reciprocal hybrids between species of *Oenothera*, *Funaria* and *Epilobium* are different in appearance. Some of these differences are known to be due to differential gametic or zygotic viability. Others depend on the interaction of one factor content with either of the two different cytoplasm of the parents. The "factors" in the cytoplasm are known as plasmons (Correns, 1909 *b* and Wettstein, 1924 *a*).

Several examples of cytoplasmic influence have been found by Wettstein (1924 *a*, 1927, 1928) in the mosses. The diploid hybrid sporogonia of *Funaria hygrometrica* \times *F. mediterranea* and tetraploid hybrid sporogonia of *F. hygrometrica* \times *Entosthodon fasciculare*, *F. hygrometrica* \times *Physcomitrium piriforme*, *Physcomitrella patens* \times *Physcomitrium eurystomum* correspond to the female parent in reciprocal crosses. The paraphysis in diploid gametophytes derived from the reciprocal crosses between *F. hygrometrica* \times *F. mediterranea* also show the influence of the maternal cytoplasm distinctly. The spores of *F. hygrometrica* \times *F. mediterranea* show two size classes in a tetrad of spores (see Fig. 1), but in the reciprocal cross they are of one size class corresponding to that of the maternal parent.

In *Epilobium*, Lehmann and Schwemmle (1927), and Åkermann (1921), report many differences in reciprocal hybrids between species. Here it appears that nuclear phenomena as well as cytoplasmic differences may be involved and more work on this genus is required.

In *Oenothera* there are two main types of reciprocal differences in species hybrids. One is due to heterozygosity and differential viability of the zygotes and gametes (see p. 277). The other is due to differences in the plasmon, and this only will be considered here.

If the two normal green species, *O. Lamarckiana* and *O. Hookeri*, are crossed, and if the mother is *O. Lamarckiana*, the hybrid *velutina* (see p. 279) is pale green and often dies. Those plants which survive are generally variegated. The reciprocal hybrid (*O. Hookeri* \times *O. Lamarckiana*) *velutina* is almost always normal green, but a

TABLE 6

Cytoplasmic Influence upon Factor Expression in
Linum usitatissimum

Plants with cytoplasm from tall \bigcirc				Plants with cytoplasm from procumbent \square			
		♀	M.S.			♀	M.S.
F_1	$\bigcirc_{mm} \times MM$	175	0	F_1	$\square_{MM} \times mm$	188	0
F_2	$\bigcirc_{Mm} \times Mm$	126	0	F_2	$\square_{Mm} \times Mm$	1,213	341
					<i>expected</i>	1,165	388
				F_1	$\square_{Mm} \times mm$	61	77
					<i>expected</i>	69	69
				$(\square_{mm} (M.S.) \times MM) \times mm$		62	41
				<i>expected</i>		51.5	51.5
				$\square_{mm} (M.S.) \times Mm$		134	145
				<i>expected</i>		139.5	139.5
				$\square_{Mm} \times Mm$		1,285	422
				<i>expected</i>		1,272	424

few individuals have light green flecks on the cotyledons. *O. suaveolens* \times *O. muricata* gives *flavicurva*, which has no chlorophyll, while the reciprocal hybrid (*flavicurva*) is usually green with white spots.

Bateson and Gairdner (1921) found that the cross, procumbent \times tall *Linum usitatissimum* gave 25% male steriles in the F_2 , while

the reciprocal cross gave only hermaphrodites. A male sterile $F_2 \times$ tall hermaphrodite gave all male steriles. A male sterile $F_2 \times$ procumbent hermaphrodite gave all hermaphrodites and segregation of 3 hermaphrodites to 1 male sterile in the following generation. Male sterile \times (T \times P) F_1 gave 50% of male steriles and hermaphrodites.

Chittenden and Pellew (1927), Wettstein (1928 a), Gairdner (1929), and Correns (1928 a) all suggest that the interaction of cytoplasmic and nuclear reactions will account for such differences in reciprocal crosses.

In *Linum* a recessive factor m for male sterility may be present in the tall plants which in tall cytoplasm \bigcirc gives only hermaphrodites. When the cross procumbent \times tall is made the factor m may be combined with procumbent cytoplasm \square so that \boxed{mm} is male sterile and $\bigcirc mm$ is hermaphrodite. Table 6, Gairdner (1929), illustrates the expected and observed results in the various crosses.

A similar behaviour is found in *Geranium Endressi* \times *G. striatum* and a similar explanation was suggested by the late W. C. F. Newton. *Satureia hortensis* is a gynomonoeious species. Correns (1928 b) obtained only hermaphrodites from selfing hermaphrodites and gynomonoeious and hermaphrodites from crossing a female with a hermaphrodite. He suggests that there is a cytoplasmic difference between the two sex forms.

East (1932) found that in crosses between *Nicotiana Langsdorffii* and *N. Sanderæ* the self-sterility factors S_{1-15} other than S_i gave rise to male sterile plants when *N. Langsdorffii* cytoplasm was present, and hermaphrodites in the presence of the cytoplasm of *N. Sanderæ*. The factor Z , together with the factor S_i , induces the formation of chlorophyll in the corolla of plants with cytoplasm of *N. Langsdorffii*, but not with cytoplasm of *N. Sanderæ*. The combination of factors C,P, C,D and C,D,P, gives dark anthers in cytoplasm of *N. Langsdorffii* and light-coloured anthers in cytoplasm of *N. Sanderæ*.

Perhaps one of the most interesting cases is that of *Vicia Faba* described by Sirks (1931). In addition to factors $C_1C_2C_3$ which cause

a difference in the colour of the plants there is a variegation based on one factor **V** which is dominant to **v** for green. Sirks found that segregation into a ratio of $1VV : 2Vv : 1vv$ was the normal behaviour of typical **Vv** plants, but in cytoplasm of plants with the C_3 (subtypical) factor it was found that **V** was cast out or was not viable in one of the sexes, thus producing a permanent $1Vv : 1vv$ segregation. In cytoplasm of variegated plants the **v** factors are eliminated in one of the sexes and an apparently pure breeding strain consisting of **VV** and non-segregating **Vv** plants is produced.

Vicia Faba has been divided into the varieties *major* and *minor*. Sirks found that in the cytoplasm of *major* the segregation of six factors belonging to one linkage group (carried by one pair of chromosomes) was normal. These six dominant factors were introduced from the *major* variety into the cytoplasm of *minor*. No plants homozygous for these six dominant factors were found in the progeny of this hybrid with *minor* cytoplasm. This behaviour was accompanied by about 25% abortion of seeds. Sirks rejects the idea that there is a lethal factor in the chromosome carrying these six factors which acts in *minor* cytoplasm, on the grounds that crossing over between the lethal and some of the six factors should have been observed. He puts forward a suggestion that the chromosome bearing this linkage group is impregnated with some lethal character which acts in *minor* cytoplasm. These valuable data of Sirks may possibly be found to be similar to the cases of genotypic control of the chromosomes mentioned by Darlington (1932 b).

CONCLUSIONS

Consideration of the foregoing facts indicates at once that the original idea of one character—one factor, is false. It will also be apparent that the factors which are isolated by crossing two plants with alternative characters, such as white flowers and red flowers, are only known by their differential effect on that character. Further, their action depends on the presence of many, if not all, of the remaining factors present in the plant.

Naturally many factors are unknown, since there is either no allelomorph or the different effects of the two have not been detected. The factors which do not show differential action

between allelomorphs may possibly be those which are essential for the life and existence of the plant. Indeed, it is probable that many of the lethal factors isolated by genetical study are allelomorphs of these "vital" factors. Sometimes the so-called lethal factor may in reality be an absence of the genetic material. In some cases (sub-lethal factors) the effect in terms of development of the plant can be analysed, but in the more extreme cases the action of the factor is so rapid that the influence of either the lethal factor or the vital allelomorph cannot be analysed.

The development of the plant is dependent on the factors contained in it. At every stage from the original one-celled zygote to the production and survival of the gametes, the development of the plant is controlled by the genetic factors which are contained in the nucleus. Haldane (1932) has given an interesting classification of factors which is based on their time of action. While much more requires to be done in the investigation of the time of factor action, it is apparent that the acceleration or deceleration of the action of a factor creates considerable derangement of the ontogeny (e.g., Mangelsdorf's factors for premature germination). The train of factor actions is so balanced that the influence of a factor takes effect at a definite point (or points) in the development of a definite part (or parts) of an organism. Thus the factor *h* in *Primula sinensis* affects the cotyledons causing them to be yellowish, and the distribution of the colour in the petals (de Winton, unpublished). Another factor which controls length of style acts definitely during the development of the flower. The reactions between the genetical constitution of the plant and the external environment determine the phenotype (or outward appearance and physiological characteristics) of the plant.

Some geneticists have raised objection to the use of such phrases as "interaction of factors," "unit characters," and "Tu as a factor for Tunicate ear." Some geneticists even enumerate all the known factors in a plant when they are describing the monofactorial segregation of one of them. We agree that the underlying viewpoint is sound, that without the presence of all the genetical factors (and environmental factors) the factor being considered would be inactive. Nevertheless, the mnemonic system of symbols for

factors and the use of abbreviated phrases is extremely useful, and in our opinion justified.

The terms dominant, recessive, epistatic, hypostatic, complementary, polymeric, duplicate (see p. 218), pleiotropic, lethal, sub-lethal and others are useful for purposes of description of the phenotypic effects and actions of the factors. It should be emphasised, however, that the nature of the factor itself is not designated by these terms. Further, there is an almost continuous series grading from one type of inheritance to that of another. For example, two factors together may give a 15:1 ratio or a 9:3:3:1 ratio or a 9:3:4 ratio or a 9:7 ratio or a 12:3:1 ratio. In the first case each factor is completely dominant over the recessive allelomorph, and the phenotypic effect of both factor actions is similar. In the second case the expression of the actions of the two factors is different. In the remaining cases there are varying degrees of expression dependent on the ability of the factors to determine characters alone or in conjunction with the complementary factor. These ratios depend on (1) our ability to separate one class of plants from another, *e.g.*, Blakeslee (1921 b) was able to transform a 9:7 ratio into a 9:3:4 ratio by treating the bud cones of *Rudbeckia* with caustic potash, (2) the relative dominance of the factors over their allelomorphs, and (3) the genetic background of all the factors to the one considered. The character expression of a factor A may or may not be distinguishable from that of a unless certain other factors are present.

CHAPTER II

THE CHROMOSOME THEORY OF HEREDITY

Introduction—Mitosis—Meiosis in Diploids and Polyploids—Precocity Theory of Meiosis—Chromosome Disjunction and Segregation—Linkage—Cytological Basis of Genetical Crossing-over—Classical and Chiasmatype Theories—Segmental Interchange—Double Crossing-over—Variation in Linkage Values—Conditions of Genetical Crossing-over—Chromatid Segregation—Genetical and Cytological Chromosome Maps.

Introduction. The discovery of van Beneden in 1883 that the nucleus of the egg and the nucleus of the spermatozoon of *Ascaris* each contained half the number of chromosomes of the nuclei in the body cells, initiated a series of investigations on the physical side of the problem of heredity. Strasburger (1888) showed that the reduction in number of chromosomes took place in the megasporocytes and microsporocytes of plants. Weismann and Strasburger independently concluded that the nucleus was "the vehicle of heritable variation" (1884-1885), while Strasburger (1894) postulated that there was a reduction in the number of chromosomes at sporogenesis in all organisms which exhibited sexuality. Rückert (1892) suggested briefly that a conjugation and disjunction of paternal and maternal chromosomes took place at meiosis, while Montgomery (1901 *a, b*), without the knowledge of Mendel's laws of segregation, emphasised the presence of paternal and maternal homologous chromosomes in diploid groups, and accepted their conjugation and disjunction in pairs at meiosis.

The parallelism between the pairing and disjunction of chromosomes at meiosis and the segregation of the factors at the maturation division, was suggested by Strasburger, Correns, Guyer and Cannon about 1901, but Sutton (1903) and Boveri (1904) first clearly realised the significant correspondence between the cytological phenomena and Mendelian segregation. Boveri (1904), by some remarkable experiments, showed that the development of an organism was influenced by the chromosomes, and that the chromo-

somes in one organism were qualitatively diverse in effect on the characters of the organism.

Much later, Carothers (1913, 1917, 1921, 1926), Wenrich (1917), Navashin (1925 *a, b*, 1931 *a*) and Sveshnikova (1928) have published results independently which demonstrate that the segregation of the chromosomes to the progeny is strikingly similar to that observed for genetical factors.

Carothers (1913, 1917) found that the disjunction of one pair of chromosomes in *Trimerotropis* was not influenced by that of a different pair. It had been known for some time through the work of Wilson *et al.* (see Wilson, "The Cell") that the pair of chromosomes which were related to the determination of sexuality were heteromorphic in many animals. At meiosis, the difference in size or shape enabled observers to see that one chromosome of the pair might pass to one or other of the poles at the first of the two divisions of meiosis (heterotypic), and hence to the daughter cells, while the other member of the pair would go to the alternative pole. It will be seen that a ratio of 1 : 1 will thus be mechanically obtained, in respect of the members of the sex chromosome pair, for distribution to the daughter cells and the gametes.

Two pairs with heteromorphic members are, however, necessary to prove that disjunction of different pairs of chromosomes is at random and independent.

In *Trimerotropis* Carothers found that in addition to the sex chromosome, which lacked a partner in the male sex, XO type, one pair of chromosomes had unequal members, which could be distinguished by their shape and the position of the attachment to the so-called spindle fibre. She found that out of 300 metaphase plates of reduction divisions 51.3% had the larger member of the dimorphic pair going to the same pole as the sex chromosome and 48.7% had the smaller member of the heteromorphic pair accompanying the sex chromosome. This is remarkably close to the expected 50% distribution, expected on random and independent assortment.

Similar observations were furnished by Wenrich (1917) in *Phrynotettix magnus* and by Robertson (1915, 1916) in the *Tettigidae* and *Acrididae*. Later Carothers (1917) obtained data involving four different "pairs" of chromosomes in *Trimerotropis fallax*.

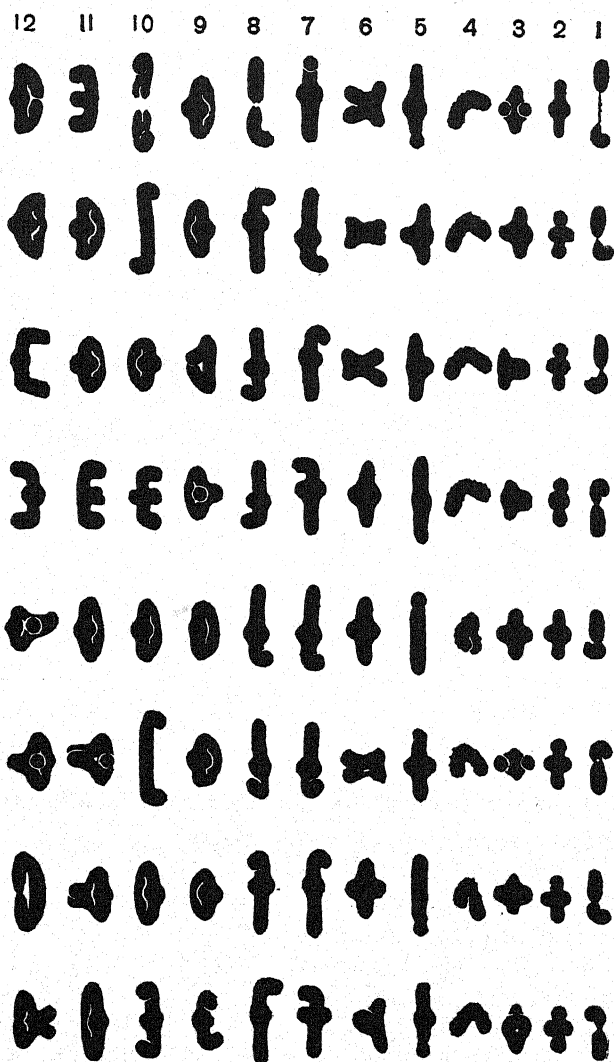


FIG. 9.—Lateral views of chromosomes in the first spermatocyte of eight cells from a single individual. The chromosomes of each cell are arranged horizontally in a series according to size. The vertical rows represent the same pair of chromosomes in different cells. Note the difference in shape of separating members in pairs Nos. 1, 7 and 8 and the unpaired sex chromosome, No. 4. (Carothers *ex* Babcock and Clausen, 1927.)

Table 7, constructed from observations on 100 first divisions (which would give rise to 200 second divisions), shows the closeness of observation and expectation. The chromosomes numbered 1, 7, 8 and 4 (the unpaired sex chromosome) in Fig. 9 were those studied. It will be seen that size and shape difference are pronounced.

We see therefore in the disjunction of chromosomes at meiosis a close similarity to the segregation of factors. In both cases the factor and chromosome separates from its counterpart which has

TABLE 7

Distribution of Members of Heteromorphic Pairs of Chromosomes in a Single Individual of Trimerotropis fallax (Data from Carothers ex Babcock and Clausen, 1927)

Type.	Expected.	Observed.
A given V (Nos. 1 or 4)	$\frac{1}{2} \times 200 = 100$	100
Only one V	$\frac{1}{4} \times 200 = 50$	48
Two given Vs (Nos. 1 and 4)	$\frac{1}{4} \times 200 = 50$	46
Two given Vs (Nos. 7 and 8)	$\frac{1}{4} \times 200 = 50$	47
Any two Vs	$\frac{3}{8} \times 200 = 75$	84
Three given Vs (Nos. 1, 7, 8)	$\frac{1}{8} \times 200 = 25$	22
Three given Vs (Nos. 4, 7, 8)	$\frac{1}{8} \times 200 = 25$	21
Any three Vs	$\frac{1}{4} \times 200 = 50$	48
Four Vs	$\frac{1}{16} \times 200 = 12\frac{1}{2}$	8

been derived from a different formative gamete, and passes to the opposite pole and hence to a different gamete at random. It can be shown in several ways that the chromosome derived from a parent passes into the offspring and is uninfluenced by the passage through the gametophyte.

Navashin (1927 a, b) crossed *Crepis tectorum*, having eight chromosomes in the somatic tissue, with *Crepis alpina* ($2n = 6$). All the chromosomes can be identified by their shape and size. Gametes were produced by the hybrid ($2n = 7$) with the parental chromosomes (4 and 3), and these could again be recognised in the second generation. The chromosomes had passed through the hybrid and appeared in the succeeding generation without change.

Fig. 10 shows that the chromosomes of the parental species *C. capillaris* ($2n = 6$) and *C. aspera* ($2n = 8$) are recovered in the hybrid ($2n = 7$).

In a considerable number of cases the chromosome complement of one species is found to be different from that of a related species. One or more chromosomes may differ in size, or in the position of the attachment constriction (see p. 75), or there may be differences in the number of chromosomes. For example, Navashin, Babcock, Hollingshead and others can recognise the individual chromosomes of *Crepis* and show that there are differences in size, shape and number between different species. In one species the characteristics of the chromosomes are constant, except in those cases where genetic variation is present (cf. Darlington, 1932 *a*).

When aberrations occur, such as breaking of chromosomes, it is found that the descendants exhibit the peculiarities expected. For example, the *X* chromosome of *Drosophila melanogaster* was broken into two portions, one of which was attached to the fourth chromosome. In some of the progeny the two half chromosomes were present; one half was still attached to the fourth chromosome (Stern, 1931).

It will be realised that the nucleus which initiates the new zygote results from the fusion of a paternal and a maternal nucleus. The chromosomes thus included in the first cell of the zygote are propagated without qualitative or quantitative change to all daughter cells of the somatic tissue by mitotic division.

MITOSIS

The mechanism of *mitosis* or karyokinesis was first identified as such by Schneider (1873), Strasburger (1872, 1878), van Beneden (1883), Flemming and others, while the name mitosis, now commonly used, was given by Flemming (1879, 1880, 1882), who showed the characteristic splitting of the chromosomes. The daughter halves of the longitudinally split chromosomes were seen to pass to opposite poles by van Beneden and Heuser about 1884, in animals and plants respectively.

The zygotic cell of the normal diploid plant contains an even number of chromosomes, each type of chromosome being repre-

sented twice. Hence, the chromosome complement of one plant can be separated into two similar sets of chromosomes. One member of each pair of chromosomes has been derived from one parent and the other from the alternative parent.

Description of Mitosis.

The nucleus in the resting stage appears to contain a fine network or reticulum which at the beginning of the division is resolved into threads which appear to be double longitudinally along their whole length. This prophase stage proceeds and the threads shorten and thicken. They are arranged on an equatorial plane in the nucleus and the nuclear membrane disappears. Fine fibres from the poles appear to become attached to a definite position on the chromosomes (metaphase stage). These spindle fibres, which are seen in material which does not

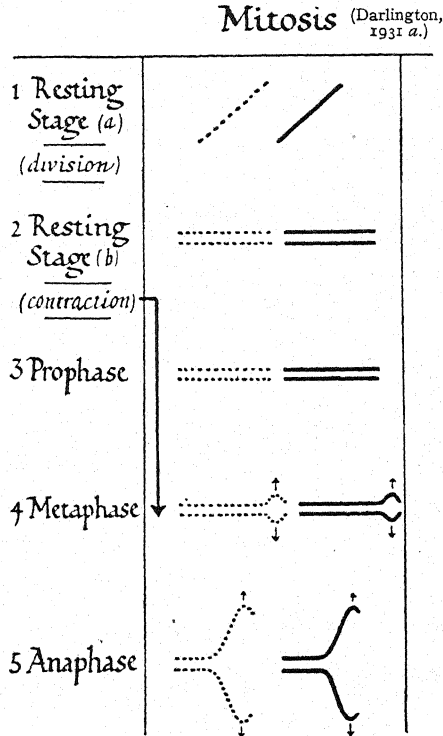


FIG. 11.

show the best fixation, appear to correspond to the highly viscous area found in living material by micro-dissection methods. The fibres are probably fixation products of some (possibly) physical structure of the area.

The paired half chromosomes, or chromatids, separate first at the place where the spindle fibre is attached to the chromosome. This point is generally constricted and is sometimes called the attachment constriction. Present-day methods of technique have enabled

cytologists to determine that these constrictions, as well as secondary constrictions, at other places on the chromosome, are constant characteristics of a particular chromosome. Satellites or trabants which presumably result from a sub-terminal constriction are also diagnostic features of chromosomes. All somatic cells of one plant have similar chromosome complements, and it is therefore reasonable to suppose that the chromosome does not lose its individuality during the interphases.

After metaphase the split chromosomes separate and pass to opposite ends of the spindle area (anaphase), and in the Angiosperms, with few exceptions, a cell wall is laid down between the separated nuclei along the spindle fibres, probably by a process of coagulation.

Recent advances in cytology have been largely due to improvement in technique. Older methods of fixation and staining have been replaced or improved, with the result that more critical observations have been made. Hence cases which did not seem to agree with the general interpretation have been brought into line. For example, it was imagined that amitosis or division of the nucleus without splitting of the chromosomes was a normal process. It is now known that amitosis only normally occurs in tissues that will supply reserve material on later degeneration, *e.g.*, tapetum and young vascular tissue.

Bělár (1928) made microphotographs of a living cell and of the same cell after fixation and again after staining (Fig. 12). He thus showed that good fixation and staining greatly facilitates the study of the chromosomes without distorting the configurations of the living cell. Further, the processes of mitosis and meiosis have been shown (in living material) to be comparable with those seen in fixed material.

MEIOSIS

Sexual reproduction, by which most plants produce offspring at some period in their life history, consists essentially in the fusion of two nuclei—the male and female gametes. Since the chromosomes are definite and autonomous bodies, the zygote and the succeeding sporophyte has the sum of the chromosomes contributed by the gametes. If the chromosome number of the species as a whole is to be constant, there must be a process by which the chromosome

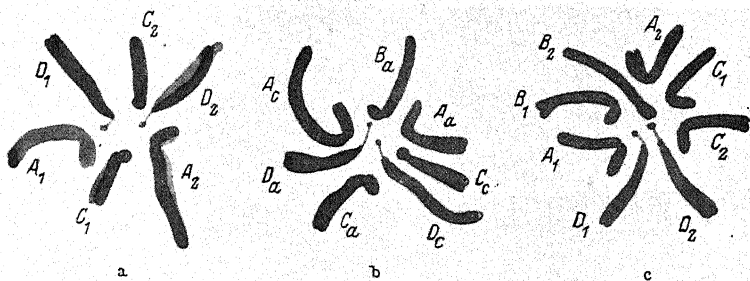


FIG. 10.—Somatic chromosomes of (a) *Crepis capillaris*; (b) F₁ *C. capillaris* × *C. aspera*; (c) *C. aspera*. The index letters c and a indicate the parental chromosomes in the hybrid. (Navashin, 1927.)

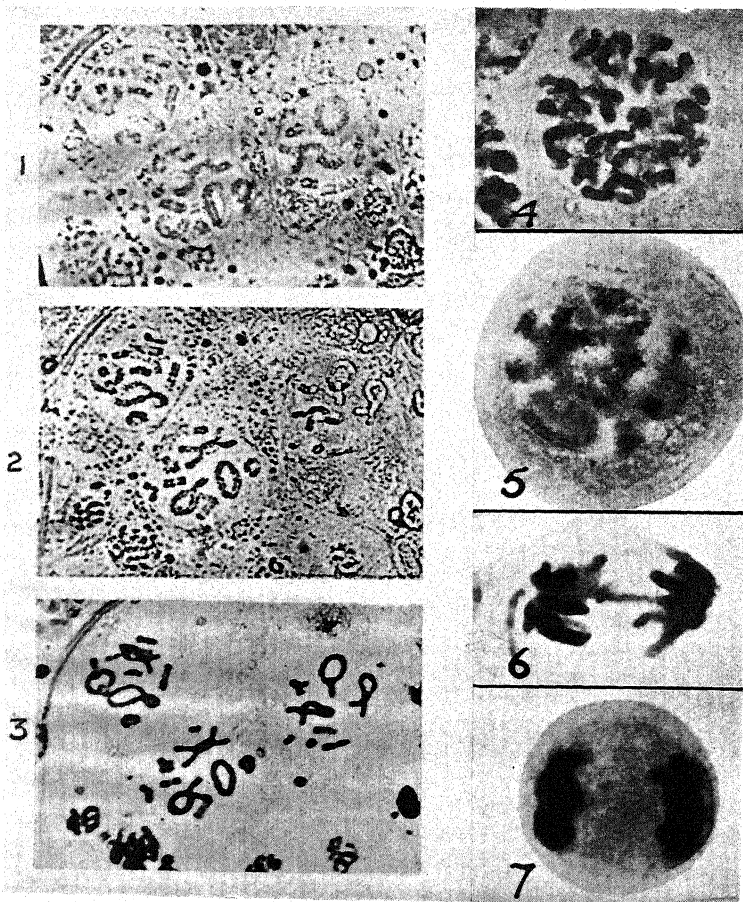


FIG. 12.—1-3. Diakinesis in *Stenobothrus lineatus*. (From Bělár, 1927.) 1. Living cells. 2. The same cells after fixation with osmium tetroxide vapour and Flemming. 3. The same cells after staining with Giemsa-Romanovsky. 4-7. Photographs of living chromosomes of *Melanoplus femur rubrum* (Orthoptera) at meiosis taken by the method of Bělár (1927).



number is halved during gametogenesis. The place in the life cycle, at which the reduction occurs has already been indicated in Fungi, mosses, ferns and Angiosperms.

Meiosis usually consists of two divisions—the first, or heterotypic division, in which the reduction of the number of chromosomes takes place, and the second, or homotypic division, in which the products of the first division are propagated as in mitosis. The essential difference between meiosis and mitosis (following Darlington, 1931 *a*) is that in mitosis every division of the nucleus is accompanied by a division of the chromosomes, but in meiosis there are two divisions of the nucleus with one of the chromosomes.

Description of Meiosis. For a full description of meiosis reference should be made to Darlington's book in this series. Only an outline sufficient for genetical purposes will be given here.

Diploid Plants. In the early prophase, fine leptotene threads each representing a whole chromosome become aligned in pairs (zygotene stage). Each pair of threads represents one chromosome derived from the mother and one chromosome derived from the father. At the following pachytene stage the chromosomes split lengthwise into

*Diagram of Reduction of Chromosomes
in Germ-Cell Formation.* (Darlington,
1931 *d*.)

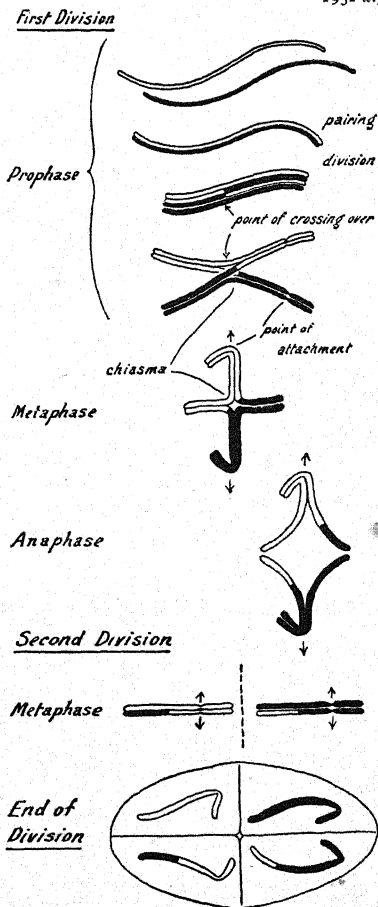
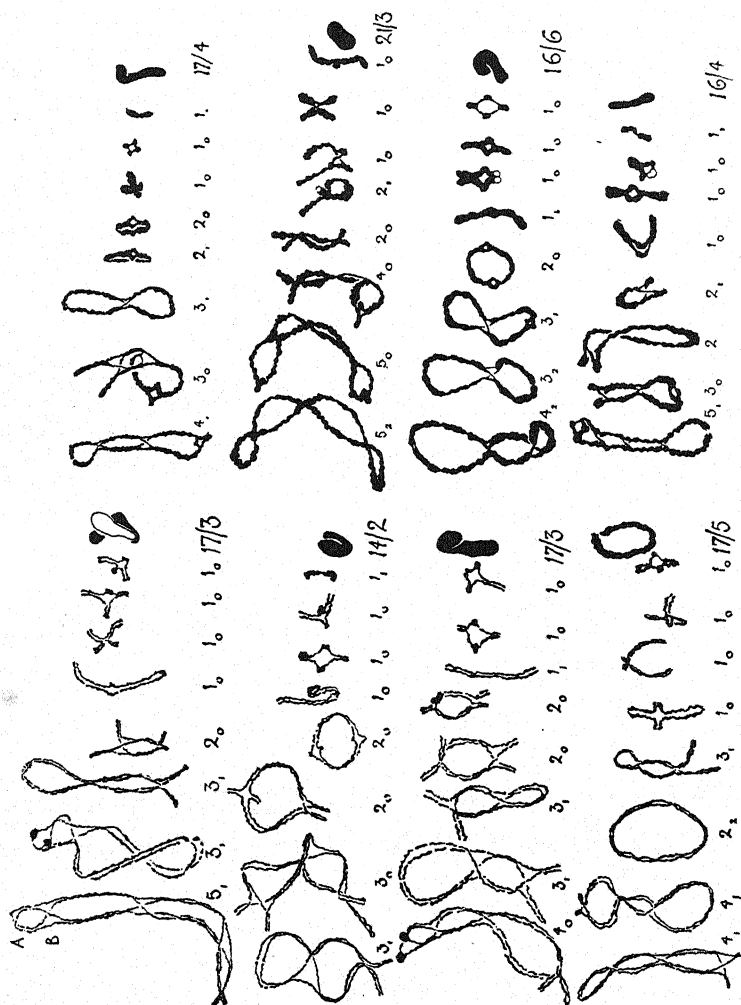


FIG. 13.



two *chromatids* or "half chromosomes." Immediately afterwards the chromatids take up a looped appearance characteristic of the diplotene stage. At pachytene the chromosomes are associated in pairs, while at diplotene the chromatids are associated in pairs. At diplotene the chromatids assort in pairs in such a way that in

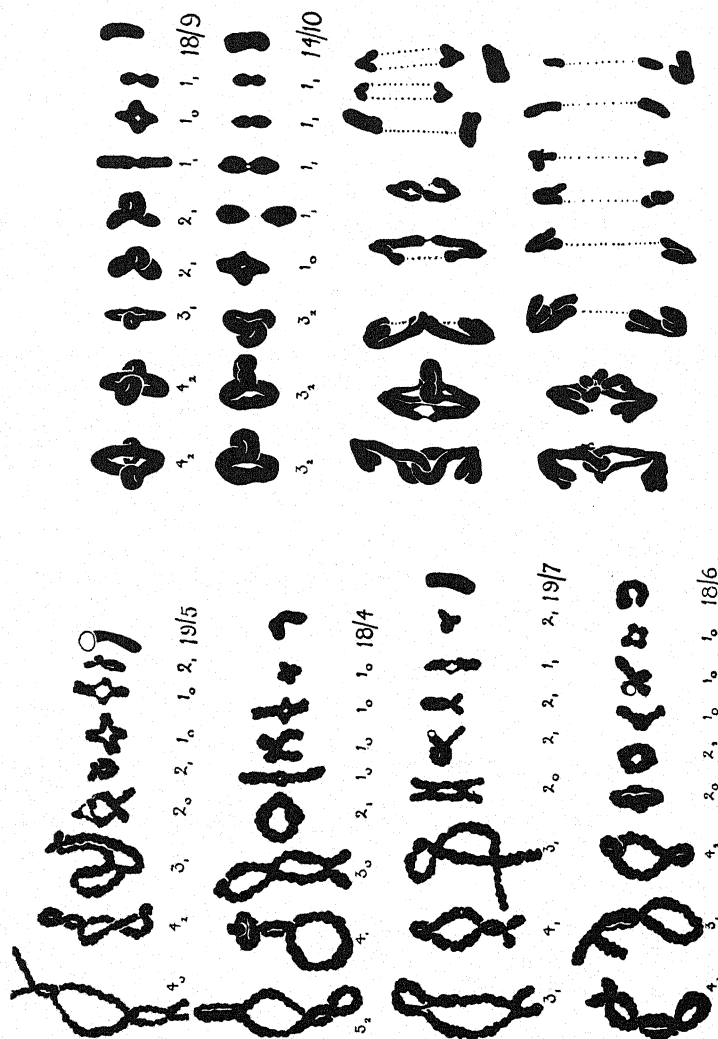


FIG. 14.—Meiosis in *Stenobothrus parallelus*. (Darlington and Dark, 1932.)

one part of their length two chromatids are associated but at another part each is associated with a different chromatid (see Fig. 14). The point of exchange of partners is termed a *chiasma* (Janssens, 1909, 1924).

The chromatids exchange partners at random, and chiasmata will be formed at random throughout the length of the associated chromatids. The number of chiasmata will be proportional to the chromosome length within certain limits (see later).

The accompanying graph (Fig. 15) from Darlington (1931 *a*) illustrates the ranges in chiasmata frequency of chromosomes of different length in *Vicia Faba* (Maeda, 1930 *b*), *Fritillaria imperialis*

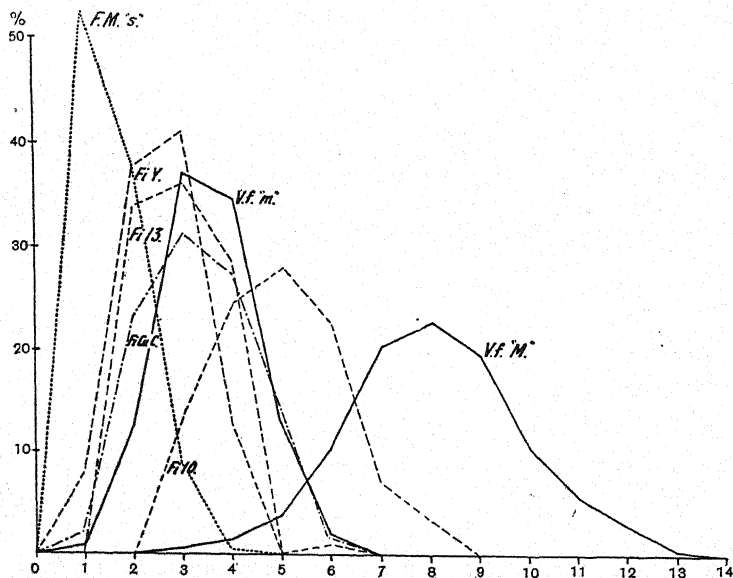


FIG. 15.—Chiasmata in *Vicia* and *Fritillaria*. (Darlington, 1931 *a*.)

(Darlington, 1930 *c*) and *F. meleagris* (Newton and Darlington, 1930). The chiasmata frequencies of the *M* and *m* chromosomes in *Vicia Faba* are entirely different; the *M* chromosome is twice as long as the *m* chromosome. This subject will be returned to under genetical crossing-over.

Linear contraction of the four chromatids of a bivalent (the two paired chromosomes of maternal and paternal origin) takes place. At the same time the chiasmata decrease in number to a greater or less extent until the stage of diakinesis, where the bivalents

lie at random in the nucleus. Metaphase follows with the arrangement of the bivalents upon the equatorial plate. At anaphase the two pairs of chromatids separate from one another and pass to opposite poles of the spindle area. In this way the number of the chromosomes is halved and the maternal and paternal parts of chromatids are disjoined.

Chiasmata and Chromosome Pairing. Darlington has pointed out that metaphase pairing results from the retention of chiasmata formed at an earlier stage. In other words, a bivalent of four chromatids holds together until metaphase by the exchange of partners among the chromatids.

It has been said that the number of chiasmata formed at prophase is sometimes reduced continuously until diakinesis. This takes place by the movement of the chiasmata away from the point of attachment (attachment constriction) to the ends of the chromosomes where successive chiasmata replace each other. There must be at least one chiasma at metaphase to hold the four chromatids together. Therefore there must be some cause for the retention of the final chiasma where the terminalisation is extensive.

When interstitial chiasmata are found at anaphase (*i.e.*, median chiasmata which have not terminalised between prophase and early metaphase) the chiasmata separate without breaking. Hence, in *Pisum sativum*, *F. meleagris* and other plants where terminalisation is slight or absent, anaphase configurations are observed which reflect the previous exchange of partners of the chromatids. This proves that the looped arrangement of the chromatids is due to changes of association and hence to chiasmata.

MEIOSIS IN POLYPLOIDS

The cytological investigation of forms with more than two sets of homologous chromosomes has been of much value in the hands of Belling and Darlington. In a normal diploid plant each maternal chromosome has a paternal homologue but in a polyploid there may be more than two homologues present.

In these forms trivalents (three chromosomes), quadrivalents (four chromosomes) and associations of greater numbers of homologous chromosomes may be found (see Fig. 16). The

DIAGRAM TO ILLUSTRATE THE PAIRING OF CHROMOSOMES IN DIPLOID
AND POLYPLOID TULIPS AND HYACINTHS

(A) Pairing of Twos

(B) Pairing of Threes

(C) Pairing of Fours

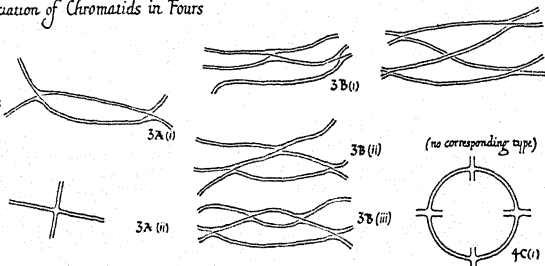
1 Zygotene

Association of Chromosomes in Pairs

2 Pachytene

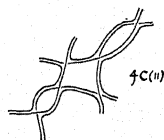
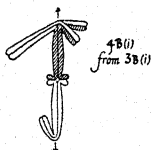
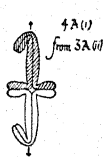
Association of Chromatids in Fours

3 Diplotene
to
Diakinesis

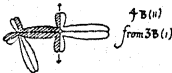
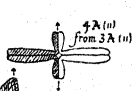


4 Metaphase

(i) Division reductional



(ii) Division equational



5 Anaphase

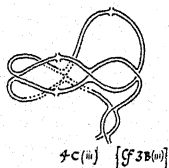
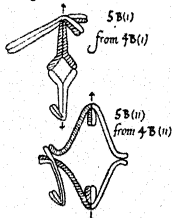
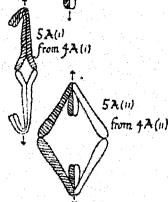


FIG. 16. (Darlington, 1929 b.)

important and fundamental point is that *never more than two chromosomes are associated at any one point*. Pairing between two chromosomes at one point may not greatly influence pairing between one member of this association and a different chromosome

at another point (see later and Darlington and Mather ("Cytologia"—in press), and Stone and Mather ("Cytologia"—in press) for a fuller discussion). Hence, in a triploid two chromosomes may be in association at one point, while at another point one may be involved with a third. After zygotene pairing between chromosomes two at a time, chiasmata are formed between the paired parts. Both qualitative and statistical analyses are being made on the behaviour of chiasmata with interesting and important results (see Darlington, 1932*a*).

After the heterotypic division, a homotypic division follows almost immediately. This division is similar to a mitotic division. It is believed that the second or homotypic division which leads to the separation of the paired chromatids is precipitated by the fact that the chromosomes split into chromatids prior to the first or heterotypic division but do not separate at that division.

Hence, in meiosis we have two divisions of the nucleus with only one division of the chromosomes.

Precocity Theory of Meiosis. Darlington supposes that meiosis is a precocious mitosis. There is evidence that the identical chromatids (those derived from one chromosome) do not separate (or perhaps even split) at the attachment constriction until the homotypic division but remain together at the heterotypic division. It is supposed that prophase of meiosis is initiated before the chromosomes split as they do prior to prophase in normal mitosis. The chromosomes therefore pair *inter se* instead of the chromatids as in prophase of mitosis. Later the chromosomes split into chromatids, and it is believed that these also pair under the same influence of normal mitotic behaviour. If this precocity theory is correct, as we have reason to believe, it has far-reaching importance from the evolutionary point of view. A reason is provided for the appearance of meiosis, sex and fertilisation in the animal and plant kingdoms (see Darlington, 1932 *a*).

CHROMOSOME DISJUNCTION AND SEGREGATION

Segregation depends on the disjunction of the chromosomes at the first division and the separation of the chromatids at the second division. Disjunction of the members of a bivalent will naturally

be regular and only exceptionally will both members of a bivalent pass to one pole after pairing (non-disjunction).

In trivalents, quadrivalents and higher associations of chromosomes, however, normal disjunction is less certain. Indeed, in a form such as a triploid, with an odd number of homologous chromosomes disjunction will always be irregular. In such a case the three chromosomes will either become associated and disjoin two to one pole and one to the other, or a bivalent and univalent may be formed, which again gives rise to a distribution of two and one. There is considerable difficulty in giving a convenient terminology to these cases for descriptive purposes. Non-disjunction implies that the members have paired at prophase and have passed to the same pole. Neither of the above triploid cases, however, may be true non-disjunction, since the chromosomes concerned may not have paired at all. When the trivalent is formed one may find that chromosome *B* pairs with the homologues *A* and *C* in different parts of its length and that *B* goes to one pole and *A* and *C* go to the other. *A* and *C* have not paired at prophase *inter se*, but are controlled by their associations with *B*.

Disjunction, non-disjunction and numerical irregular distribution must be distinguished, since they have distinct genetical consequences with regard to segregation. This will be referred to again under triploid and tetraploid segregation.

LINKAGE

The first law of Mendel concerning the separation of factors of one allelomorph pair corresponds with the cytological behaviour of homologous chromosomes at the heterotype division, but the second law of Mendel, namely, that each allelomorphic pair segregates independently of every other pair, implies that the plant cannot have more pairs of factors than number of chromosomes in the haploid set if factors are borne by chromosomes.

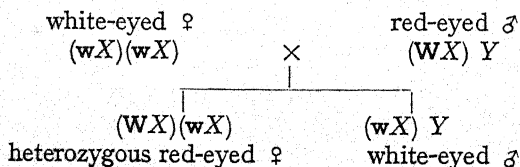
It was soon found, however, that it was necessary to modify Mendel's second law. Bateson and Punnett (1911) (see Bateson, 1930) found that the cross, blue flower (B1) long pollen (L) × red flower (b1) round pollen (l) in the sweet pea produced an F₂ of 177 B1 L, 15 B1 l, 15 b1 L, 49 b1 l, which was certainly not

a 9 : 3 : 3 : 1 ratio. They pointed out that such a zygotic series would have resulted from the selfing of an F_1 which produced gametes in the ratio 7 Bl L : 1 Bl l : 1 bl L : 7 bl l in place of the ratio 1 : 1 : 1 : 1 when two pairs of factors were completely independent. This phenomenon was called gametic coupling because the dominants tended to remain together (then considered presences according to the presence and absence theory). Later it was also found that a gametic ratio 1 Bl L : 7 Bl l : 7 bl L : 1 bl l was sometimes produced. This was called gametic repulsion, since the dominants tended to repel one another. Bateson and Punnett (1911 *a, b*) and Trow (1911, 1912) adopted the reduplication hypothesis in which it was suggested that after segregation there occurred a proliferation of gametes bearing a particular genetic complex.

Later it was found in *Primula sinensis* and other organisms that more than two factors could be linked together at one time.

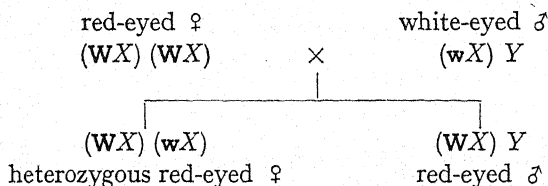
McLung (1902), Wilson and Stevens (see Wilson, "The Cell") had shown that there was a direct correlation between the morphology of a pair of chromosomes and the sexuality of several animals. The female contained, in addition to other chromosomes, two chromosomes (XX) which were similar to one carried by the male. The male possessed either another dissimilar chromosome or no other extra chromosome. Thus the female was XX and the male either XY or XO in type. Later Morgan (1911) found that sex determination and allelomorphs for red and white eyes as well as other factors were associated with this dimorphic chromosome pair in *Drosophila melanogaster*. It was found, for example, that females could be heterozygous for eye colour but males could only be homozygous for white or red eye factors and that linkage between eye colour and sex behaved in a peculiar fashion.

If white-eyed females symbolised by (wX)(wX) are crossed with red-eyed males (WX) Y the F_1 consists of red-eyed females and white-eyed males.



The factors **Ww** are transmitted along with the *X* chromosome and not independently. The *Y* chromosome does not contain factors which affect the development of eye colour and therefore the recessive **w** is able to control the colour of the eyes in the male.

The reciprocal cross, red-eyed female (**WX**) (**WX**) crossed with white-eyed males (**wX**) *Y*, gives an F_1 with both males and females red-eyed.



Thus sex determination and several mendelian factors are found to be associated with the behaviour of the dimorphic pair of chromosomes called allosomes, heterochromosomes or sex chromosomes.

Bridges (1913, 1916) found that if through non-disjunction an egg obtained two *XX* chromosomes from the female instead of one and fused with an *X* or *Y* from the male, the resulting zygote had two sets of factors of maternal origin instead of the normal one.

Morgan (1911) suggested that the facts of linkage could be brought into line with the chiasmata theory put forward in embryo by Janssens (1909) if the factors were placed in a row on the chromosomes in such a way that the position of the factor of paternal origin on the paternal chromosome corresponded to that of the allelomorph of maternal origin on the chromosome derived from the mother.

If the factors are situated on the chromosomes they should exhibit segregation phenomena of a specialised form in correspondence with the cytological facts. All factors on one chromosome should segregate independently of those on non-homologous chromosomes. The factors on one chromosome should show complete linkage unless breaks in the chromosome occur between the loci of the factors.

Obviously also, from genetical results, a breakage must take place at meiosis at a corresponding time and place on the two homologous chromosomes. This must be followed by interchange of the broken

ends to account for the recombination products of the factors. For example, if one chromosome bore the dominants **A** and **B** while the homologue bore the allelomorphs **a** and **b** in similar positions, normal disjunction of these chromosomes without interchange of parts would give gametes with the parental complements **AB** and **ab**. With interchange of the parts of chromosomes at a position between the loci of **A** and **B**, "new" chromosomes would be formed with the factorial constitution **Ab** and **aB**. These new chromosomes contain the factors in the recombined or crossed-over form.

CYTOLOGICAL BASIS OF GENETICAL CROSSING-OVER

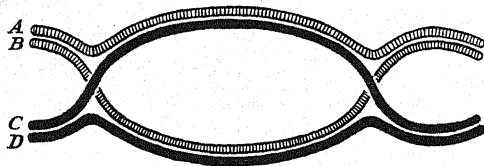
Naturally, cytologists have associated this presumption of segmental interchange of chromatids with genetical crossing-over. There is no direct evidence as to the manner in which segmental interchange takes place, but there is definite evidence from the cytology of several plants that segmental interchange occurs before metaphase.

Classical Theory. There are two views regarding the method of chiasma formation. The classical view (*cf.* Robertson, 1916, Wenrich, 1917, Wilson, 1925, Seiler, 1926, and Bělár, 1928) is that the constituent chromatids of two chromosomes do not break in forming a chiasma. Thus chromatid *A* may pair with chromatid *B* at one part of the length, and at another *A* is paired with *C* and *B* with *D*. The point of change of association is the chiasma (see Fig. 17). In this manner of formation the chiasma is constituted without previous segmental interchange between chromatids. On one side of the chiasma identical chromatids (those derived from one chromosome) will be in association, and on the other side non-identical chromatids will be in association. At which stage of meiosis segmental interchange takes place is a matter of dispute among the holders of this view of chiasma formation. Prell (1923) and Chodat (1925) are of the opinion that interchange can take place as the chromosomes disjoin at metaphase, and they have associated the observed metaphase configurations with the resolution of the chiasmata by this means.

Janssens (1924), Newton and Darlington (1929) and Sax (1930) suggest that the reduction in number of chiasmata observed between

diplotene and diakinesis is due to a movement together and resolution of some of them by segmental interchange. Several of the American workers, notably Sax (1930), favour this view, holding that the genetical data may be explained by it. Darlington (1931 *c*), however, points out that the degree of reduction of chiasmata between diplotene and diakinesis is different in different organisms, while there is no ground for believing that genetical crossing over is not of one general order. Little terminalisation takes place in *Pisum sativum* (Pellaw and Sansome, 1931), while terminalisation is strong

CLASSICAL THEORY



JANSSENS' THEORY

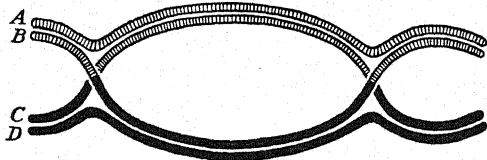


FIG. 17.—Chiasma formation.

in *Primula sinensis* (Darlington, 1931 *c*). On the above hypothesis extreme differences would be observable between the linkage phenomena in these two species. No such differences have been observed, and therefore this hypothesis requires to be supported by subsidiary ones.

Chiasmotype Theory. An alternative theory of chiasma formation and segmental interchange which appears to be supported by evidence of diverse nature is that put forward by Janssens (1924), Belling (1928 *a*) and Darlington (1930 *b*, 1931 *a*, 1931 *c*).

Janssens (1909) supposes that chiasma formation results from a previous segmental interchange (reciprocal transverse breaking and

fusion between the chromatids). He suggests various forms of chiasmatype. In total chiasmatype all four chromatid strands interchange at one corresponding point in their length; in partial chiasmatype only two chromatids interchange at any one point in the chromosome length. He also suggests that chiasmatype might occur at metaphase or at the second division, and that certain configurations in mitotic divisions might be of the same nature. Since genetic evidence indicates that crossing-over takes place during prophase of the first division, the partial and total chiasmatype are of direct interest to the geneticist (see pp. 116—121).

Belling (1928 *a*) and Darlington (1930 *b*) independently put forward views which are essentially the same as the partial chiasmatype theory of Janssens. Darlington suggests that total chiasmatype does not occur, while Belling assumes it to be very rare (see Fig. 17).

In Darlington's words (1930 *b*), "a chiasma is constituted by genetical crossing-over between two of the four chromatids taking part in it, and association at diplotene is between chromatids derived from the same chromosome." These two assumptions enable the genetical and cytological data to be brought into line.

Fig. 17 represents a bivalent immediately after chiasma formation at diplotene and illustrates the difference between this view and the classical view.

It will be seen that on the classical view each chromatid has not changed in structure but remains similar to the structure of the original somatic chromosome until segmental interchange takes place later. On Janssens theory, however, a chiasma is formed by the reciprocal interchange of two of the four chromatids and the resulting chromatids are not similar to those of the somatic complement. It should be said at once that both of these theories are in agreement with various cytological observations, but lead to different requirements in subsidiary hypotheses.

SEGMENTAL INTERCHANGE AND GENETICAL CROSSING-OVER

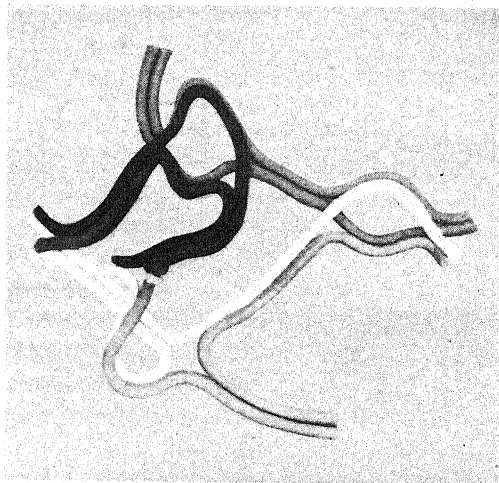
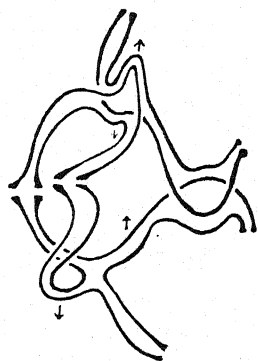
Proof that chromatid segmental interchange is associated with chiasmata formation and that it gives rise to genetical crossing-over

has been afforded in different ways by Darlington (1930 *b*, 1931 *a*), Stern (1931), McClintock (1931), McClintock and Creighton (1931) and Sansome, E. R. (1932).

In the discussion of these cases it will be seen that there is no definite evidence as to the mode of crossing-over between chromatids. Nevertheless, the theory of partial chiasmotypy affords in every case a simpler and more satisfying explanation than the alternative theory.

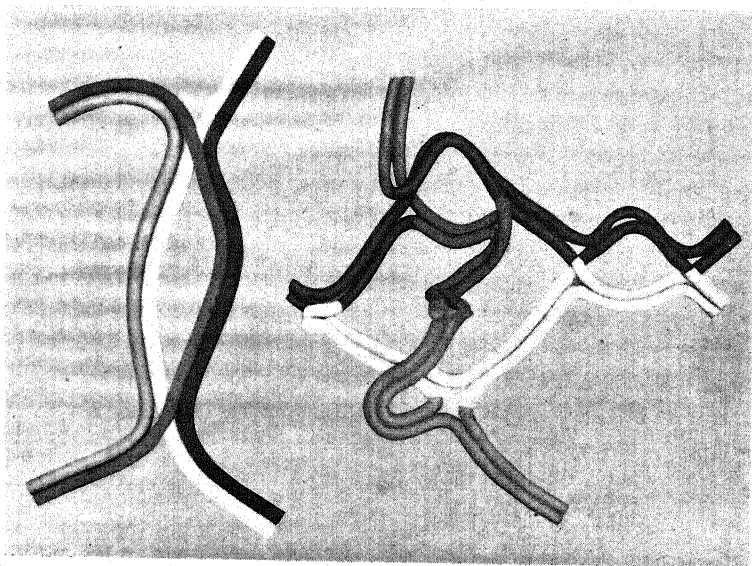
Darlington (1930 *b*, 1931 *c*) found configurations in polyploid *Hyacinthus* and *Primula sinensis* which could only result from previous cytological segmental interchange if parts of chromosomes only associate in pairs at zygotene. The configuration and the two possible interpretations of the *Hyacinthus* case are illustrated in Fig. 18. In interpretation I the constitution of the chromatids after no previous segmental interchange is such that chromatids of three different chromosomes are involved in at least one of the chiasmata. This cannot take place if chromosomes associate in pairs. Interpretation II shows that if previous segmental interchange takes place, only chromatids derived from two chromosomes are associated at any point as required by the general statement. It is highly probable that the segmental interchanges take place antecedent to chiasma formation as Janssens suggested, since a peculiar chain of circumstances would be necessary to allow segmental interchange after chiasma formation (Sax's view) to produce the same configuration without bringing into association chromatids derived from more than two chromosomes.

Darlington (1931 *b*) and Sansome, E. R. (1932), found association of chromosomes with a configuration of a figure-of-eight in structural hybrids of *Oenothera* and *Pisum*. A structural hybrid can result from crossing two races which differ in the arrangement of the parts or segments of chromosomes. [For example, one race may have the somatic chromosomes *AB, AB, CD, CD, EF, EF*, etc., while the other race has *AC, BD, AC, BD, EF, EF*, etc. The chromosome segments *A, B, C, D*, are united in the two races to form different chromosomes—relatively interchanged chromosomes. In the hybrid between these races the chromosomes will be *AB, BD, DC, CA, EF, EF*, etc.] Since homologous parts pair, a ring of four



Metaphase I.

Interpretation I.

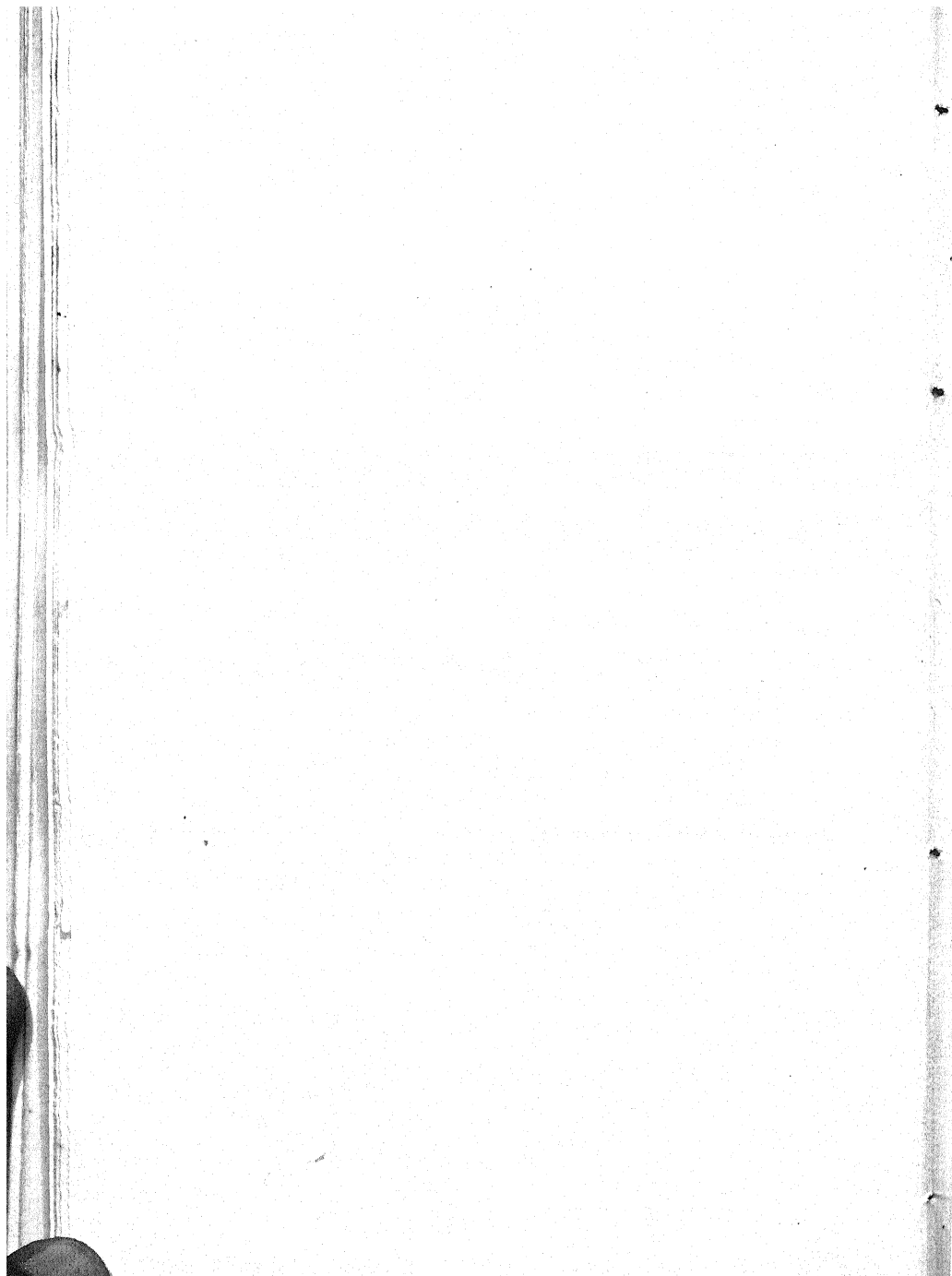


Pachytene.

Metaphase I.

Interpretation II.

FIG. 18.—Diagram of quadrivalent configuration and of pairing of chromosomes at pachytene and the possible genetical interpretations of chromatid relationships at metaphase I. (Darlington, 1930 *b*.)



chromosomes, $\overbrace{AB \quad DC}^{BD \quad CA}$ will be formed in this diploid species at meiosis. Rings consisting of larger numbers of chromosomes will be formed when more chromosome segments are inter-

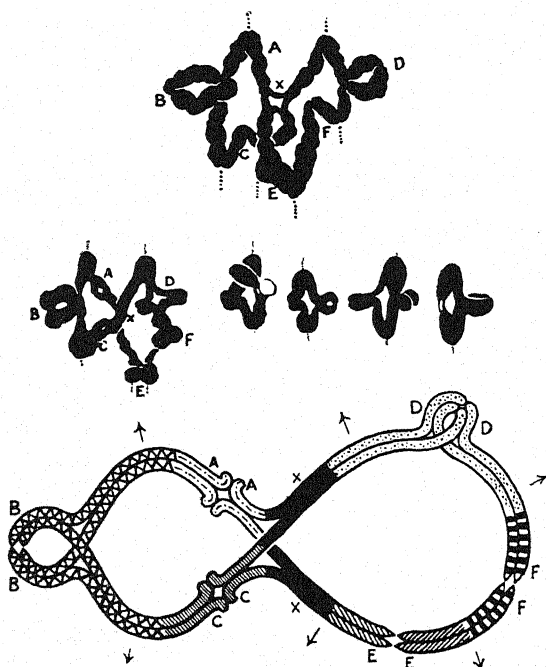


FIG. 19.—Figure-of-eight configurations with chromatid segmental interchange and diagram of the genetical interpretation. (Sansome, E. R., 1932.)

changed. For example, some *Oenothera* species have all the fourteen chromosomes in one ring.

The "figure-of-eights" found by Darlington in *Oenothera* and by Sansome in a ring of six chromosomes in *Pisum* are proofs of cytological segmental interchange for the following reasons. In the diagram (Fig. 19) representative of both *Pisum* and *Oenothera* (in *Oenothera* there are more chromosomes involved in distant parts of

the ring) it will be seen that a chiasma is present between the segments x of chromosomes AxD , CxE , and that in every case homologous parts represented by letters are pairing. This configuration cannot arise by any other method than that segmental interchange has occurred in segment x between chromatids AxD and CxE , giving rise to new chromatids AxE , CxD , if homologous parts only pair, since in the normal diploid there are only two of every part.

On the chiasmotype theory with the formation of chiasmata resulting from segmental interchange, no further hypothesis is required to account for these facts. On the alternative view it is necessary to assume that chiasmata of the compensating type (see p. 116) have been previously formed, and that chromatid segmental interchange has occurred between them. But since Sansome (1932) finds that the chiasma occurs at the x segment in 78% of cases, this assumption involving special types of chiasmata seems unlikely.

The above three cases agree in demonstrating crossing-over between chromatids without the use of genetical data. In *Zea* and *Drosophila* the demonstration is of the nature of genetical and cytological crossing-over taking place in one individual to give one product. The normal female, *Drosophila melanogaster*, has two similar rod-shaped sex chromosomes XX in addition to the autosomes, while the male has one sex chromosome X similar to that of the female together with a v-shaped chromosome Y which has a sub-median attachment constriction dividing it into a longer and a shorter arm. Stern (1931) synthesised female flies of the constitution X^b, X^d, \widehat{XY}^1 , in which X^b and X^d were separate proximal and distal halves of an X chromosome, and \widehat{XY}^1 was composed of an X joined to the long arm of the Y chromosome, the shorter arm being absent. When one half of the broken X chromosome carried the factor B (Bar eye) at 57.0 units (see p. 114) and cr (carnation) at 65.0 units and the compound chromosome \widehat{XY}^1 carried the wild type allelomorphs, crossing-over would influence the recombination of the factors and the structure of the chromosomes. Fig. 20 shows the gametic output of such a fly together with the zygotic

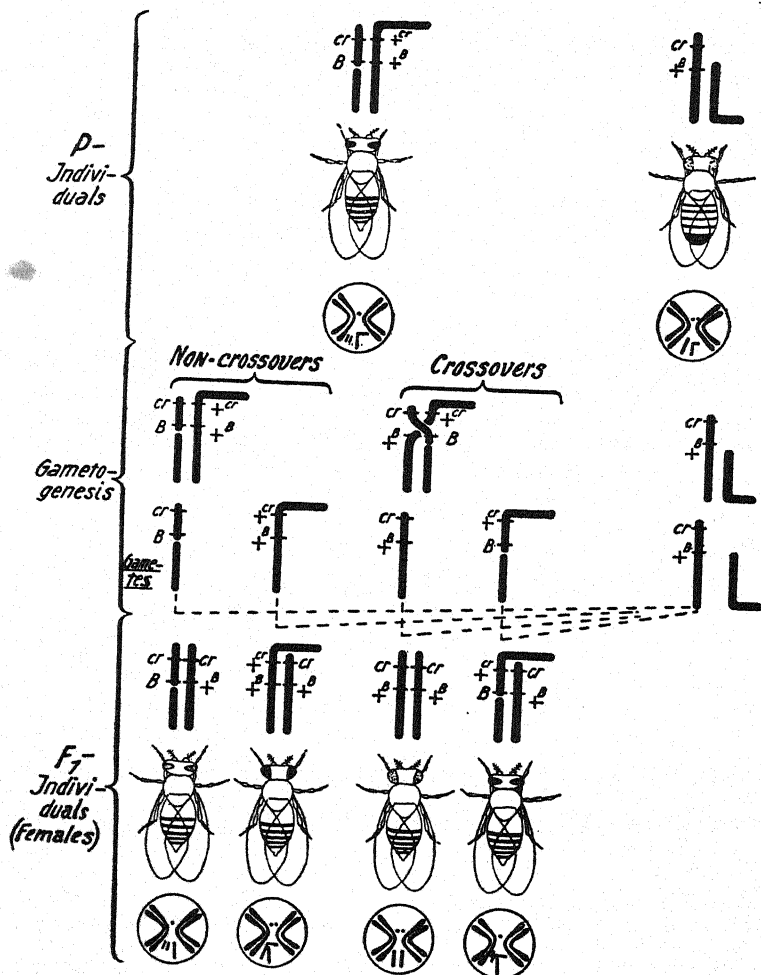


FIG. 20.—Diagram of the genetical and cytological constitution of an individual of *Drosophila melanogaster* with a fragmented X chromosome and of its progeny. (Stern, 1931.)

types obtained on crossing to a normal male carrying cr and wild type factors.

A cytological examination was made on 364 individuals of the

progeny. In 156 cases the factors **B** and **cr** had crossed over and in every case the chromosome parts were observed to have interchanged. Where no genetical crossing over took place between the factors (203 individuals) there was no observed segmental interchange.

SUMMARY OF CHROMOSOME THEORY OF HEREDITY

Evidence from diverse experiments strongly indicates the dependence and determination of genetical segregation upon chromosome behaviour. The following list summarises the main criteria which have been considered from both cytological and genetical standpoints.

(1) Genetical segregation occurs at meiosis; Bridges (1916), Allen (1917, 1919, 1924 *b*), Plough (1917, 1921), Wettstein (1924 *a*), Andersson-Kottö (1927), Kniep (1929), Gowen (1929), etc.

(2) Segregation depends on the behaviour of the chromosomes at meiosis and the number of the chromosome sets. Blakeslee, Belling and Farnham (1923), Morgan, L. V. (1925), Bridges and Anderson (1925), Karpechenko (1927 *a, b*), Newton and Pellew (1929), de Winton and Haldane (1931), Lawrence (1931 *a*), etc.

(3) Segregation takes place usually at the first division of meiosis (when the factor lies near the attachment constriction it always segregates at the first division), Carothers (1917, 1921), Wenrich (1917), Bridges and Anderson (1925), Stern (1931) Philp and Huskins (1931).

(4) Factors on non-homologous chromosomes segregate independently (except in structural hybrids). Carothers (1917), Wenrich (1917), Morgan, Bridges and Sturtevant (1925).

(5) The number of linkage groups is equal to the number of free non-homologous chromosomes. Emerson (1912) etc., Punnett (1925), Morgan, Bridges and Sturtevant (1925), Phipps (1929) *et. al.*

✓ (6) Crossing-over only takes place between homologous genetic elements, and only parts of chromosomes that are homologous can pair. Bridges and Anderson (1925), de Winton and Haldane (1931), Darlington (1931 *a*).

✓ (7) Crossing-over takes place at the four-strand stage of meiosis

between only two of the four participating chromatids at any one point. Bridges (1916), Morgan, L. V. (1925), Bridges and Anderson (1925).

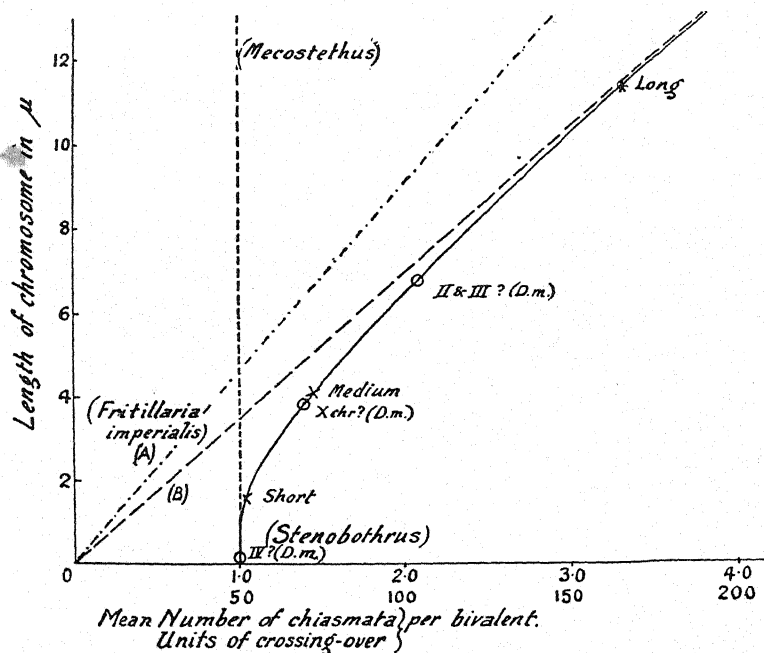


FIG. 21.—Graph showing three types of relationship possible between chiasmata or crossing-over and the length of the chromosomes: direct proportion in *Fritillaria imperialis* (two clones); fixed value with localisation in *Mecostethus* and perhaps in some *Tettigidae*; the compromise in *Stenobothrus* and perhaps in *Drosophila melanogaster* "D.m." (Darlington and Dark, 1932.)

✓(8) A chiasma is conditioned by genetical crossing-over. Darlington (1931 c), Sansome, E. R. (1932).

CONDITIONS OF CHIASMA FORMATION AND ITS BEARING ON GENETICAL CROSSING-OVER

Cytological Data. It was stated earlier that chiasmata were formed at random along the chromosome length and with a

frequency proportional to the length of the chromosome. This is probably true of chromosomes which are above a certain length, but does not apparently hold for short chromosomes.

The accompanying graph from Darlington and Dark (1932) illustrates the chiasma frequency in *Stenobothrus lineatus* in chromosomes of different lengths, together with that of *Fritillaria meleagris* and the genetic lengths of the chromosomes in *Drosophila melanogaster* (Fig. 21).

In *Stenobothrus* the chiasma frequency in the long chromosomes is proportional to the length, but in short chromosomes this is certainly not the case. Instead of a decrease in chromosome length leading to no chiasmata it leads towards the frequency of one chiasma. There is good agreement also when the genetic data of the *Drosophila* chromosomes are superimposed on the *Stenobothrus* figures.

It appears therefore that besides homology of parts of the chromosome governing chiasmata formation, a control of another type is sometimes added. This control is probably genetic in nature and nuclear in origin (Darlington, 1932 *b*). In *Fritillaria meleagris* it is found that the chromosome length does not influence the number of chiasmata. In both long and short chromosomes there is one chiasma. Either genetic control has assumed great power or the homology between two chromosomes is restricted to a portion of the chromosomes near the attachment constriction. In long chromosomes of other species, genetic control is slight, but as the influence of the homologous parts decreases (through reduction in number in short chromosomes), genetic control obtains greater influence.

The frequency of chiasmata depends on (1) the pairing properties of the chromosomes at zygotene and (2) the segmental interchanges possible in those parts that have paired. The chromosome does not behave in pairing as if made up of an infinite number of pairing particles (chromomeres), but shows that if by chance two chromomeres have paired there is a greater chance that chromomeres in the neighbourhood will be similarly paired in a similar association rather than in a different one. The chromosome behaves as if made up of a small number of "pairing blocks." Cf. Darlington and

Mather ("Cytologia"—in press), and Stone and Mather ("Cytologia"—in press).

The more recent cytological work indicates that the formation of one chiasma interferes with the formation of another to a certain extent. Haldane (1931) analysed the cytological data of eight species of plants (*Vicia Faba*, *Matthiola incana*, *Campanula persicifolia*, *Pisum sativum*, *Tulipa australis*, *Fritillaria imperialis*, and two species of *Rosa*) examined by Maeda, Darlington and others. He showed that in these eight species the chiasma frequency per bivalent did not correspond to a Poisson series as would be expected if the chiasmata were formed independently of events elsewhere. Instead it was found that the ends of the observed curve were truncated, and that there was a considerable condensation of the

TABLE 8
Maeda's Data for Long Chromosome (ex. Haldane 1931)

x	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
n obs.	0	0	0	1	3	7	13	33	39	41	28	8	8	0	0	0	0	0	0	0	0
n calc.	0.0	0.3	1.4	4.0	8.5	14.2	19.9	23.9	25.0	23.3	19.6	15.0	10.5	6.8	4.0	2.3	1.2	0.6	0.3	0.1	0.0

frequencies round the mean. Table 8 from Haldane (1931) gives the observed and calculated chiasmata frequencies per bivalent. There is a tremendous concentration at 7-10 chiasmata in the observed figures which relate to one long chromosome *M* in *Vicia Faba* (Maeda, 1930 b).

Maeda has shown that a chiasma may be formed anywhere along the length of the chromosome and is not restricted to three particular regions which the observed data in the table might suggest. Therefore Haldane concludes that one chiasma interferes with the formation of another in particular regions distal to it.

Genetical Data. There are certain genetical consequences of the chiasmotype theory which may be illustrated best by considering the phenomena of genetic linkage. Before the relationship between factor and chromosomes was realised, Bateson and Punnett discovered that the gametic output of a plant of *Lathyrus odoratus* was 7B1 L : 1b1 L : 1B1 l : 7b1 l instead of a 1 : 1 : 1 : 1 for the two factors

pairs **B1 b1** and **L 1**. This may be expressed as a $2/16$ recombination. **B1 L** and **b1 l** tend to stick together in $14/16$ of the cases and recombine in 12.5% of cases. 12.5% is the cross-over percentage and may also be written as the cross-over value 0.125 .

Sturtevant (1913) realised that if the factors were placed along the chromosome they should exhibit a spatial arrangement on an additive or subtractive plan with respect to the cross-over value. The closer the factors were together the fewer times would they recombine or cross over. If the cross-over percentage between **A** and **B** was 3% and between **A** and **C** was 4% the cross-over percentage of **A** and **C** would be 1% or 7% according as to whether **A** lay distal to **C** or between **B** and **C**. The relative distances between the factors would thus be a function of the cross-over values. He found that this was indeed the case when the cross-over value was small.

The accompanying list of factors and linkage values in plants includes the more important data on this work. It will be seen that the number of factors studied and their relationships are most fully investigated in maize.

Table of Factors in Maize, Pharbitis Nil and Lathyrus odoratus.
The Dominant Factors are represented by Capitals.

Factor symbols.

Maize (after Phipps, 1929, Hutchison, 1922, Kvakan, 1924, and others).

- | | |
|-----------|---|
| A | Anthocyanin pigment in leave-sheaths, husks and aleurone (Emerson, 1918, 1921 b). |
| ad | adherent tassel. (Kempton, 1922.) |
| an | anther ear, semi-dwarf, andromonoecious type. (Emerson and Emerson, 1922.) |
| B | intensifies plant colour. (Emerson, 1921 b.) |
| bh | blotched aleurone, expressed only in ACRBh plants. (Emerson, unpub.) |
| bl | blotched leaf. (Emerson, 1923.) |
| Bn | Brown aleurone. (Kvakan, 1924.) |
| br | brachytic culms. (Kempton, 1922.) |
| bv | brevi dwarf. (ex Kvakan, 1924.) |

Maize—continued.

- C** complementary factor for colour. (East and Hayes, 1911, and Emerson, 1918.)
- cr** crinkly leaf. (Emerson, 1921 *c*.)
- d¹** dwarf. (Emerson, 1912, and Emerson and Emerson, 1922.)
- d³** dwarf. (Demerec, 1926 *a*.)
- d¹⁻¹⁴** defective endosperm. 14 pairs of factors. (Lindstrom, 1923, Mangelsdorf, 1923, 1926.)
- f** fine striped leaf. (Lindstrom, 1918.)
- fl** floury endosperm. (Hayes and East, 1915.)
- g¹⁻²** golden plant. Two pairs of factors. (Emerson, 1912, Lindstrom, 1918.)
- gl¹⁻⁴** glossy seedling. (Kvakan, 1924, and Brunson, 1926.)
- gm** germless seeds. (Demerec, 1923.)
- gs** green striped seedlings. (Lindstrom, 1918.)
- i** inhibitor of aleurone colour perhaps allelomorphous to **C**. (East and Hayes, 1911, Emerson, 1918, and Hutchison, 1922.)
- j** japonica leaf. (Lindstrom, 1918.)
- l¹⁻²** yellow seedlings. Two pairs of factors. (Lindstrom, 1921, etc.)
- lg** liguleless leaf. (Emerson, 1912.)
- li** lineate leaf. (Emerson, 1912.)
- m¹⁻²** yellowish leaf. (Stroman, 1924.)
- ms¹⁻⁵** male steriles. (Eyster, 1931 *c*.)
- na** nana, dwarf. (Hutchison, 1922.)
- P** pericarp colour. (Emerson, 1911, Anderson and Emerson, 1923, and Anderson, 1924.)
- pb** piebald seedlings. (Demerec, 1926 *a*.)
- pg¹⁻²** pale green seedlings. (Brunson, 1924, Demerec, 1925.)
- Pl** Purple plant colour. (Emerson, 1921 *b*.)
- pk** polkadot leaves. (Eyster, 1924 *a*.)
- Pr** Purple aleurone. (Emerson, 1921 *b*.)
- pm¹⁻²** primitive sporophyte. (Eyster, 1924 *b*.) (Same as **ge¹—ge³** of Mangelsdorf, 1926.)
- R** a complementary factor for colour of aleurone; allelomorphous series (see p. 38.) (Emerson, 1918, 1921 *b*.)

Maize—continued.

ra	ramosa ear. (Gernert, 1912.)
re	reduced endosperm. (Eyster, 1931 <i>b</i> .)
rg	ragged. (Eyster, 1931 <i>c</i> .)
s	spotted aleurone. (Kempton, 1919.)
sc	scarred endosperm. (Eyster, 1922.)
sh	shrunk endosperm. (Hutchison, 1921, 1922.)
sk	silkless. (Jones, 1925.)
su	sugary endosperm. (Correns, 1901.)
ts ¹	tassel ear, pistillate plant. (Emerson, 1920.)
Tu	Tunicate ear. (Collins, 1917, and Eyster, 1921.)
ts ²⁻⁴	tassel seed. Three pairs of factors. (Emerson, 1920, and Phipps, 1928.)
tw ¹⁻³	twisted seedlings. (Kvakan, 1925.)
v ¹⁻²⁰	virescent seedlings. (Phipps, 1929.)
vp	vivipary in maize. (Eyster, 1931 <i>d</i> .)
wx	waxy endosperm. (Collins, 1909 see 1912, and Bregger, 1918.)
w ¹⁻¹¹	white seedlings. (Stroman, 1924, Lindstrom, 1918, 1924, and Demerec, 1926 <i>a</i> .)
y ¹⁻²	yellow endosperm. (East and Hayes, 1911, and Hayes and Brewbaker, 1926.)

Pharbitis Nil. (Imai, 1931.)*Linkage group 1.*

v	variegated.
C ¹	crumpled-1.
B ¹	Blown-1.
f ³	fasciated-3.
br	brown.
fd	faded.
cu	couple.

Linkage group 2.

co	cordate.
fe	feathered.

sc	semicontracted.
pc	precocious.
pl	palmate.
cp	crepe.

Linkage group 3.

y	yellow.
dy	dusky.
lt ¹	light-1.
de	deformed.
sp-r	speckled, reduced.

Pharbitis Nil—*continued*.

Linkage group 4.

ac	acuminate.
Mr ²	Margined-2.
mg	magenta.

Linkage group 5.

Ry	Rayed.
Cr	Cream.
ig	interaxil green.
sh	shrubby.
ct	contracted.
Mr ¹	Margined-1.
Ex	Expanded.
fl	flecked.
tw	tube white.
i	intense.
Mr-r	Margined-reduced.
dk	duskish.

Linkage group 6.

sp	speckled.
w ¹	white-1.
Mr-f	Margined-fluctuated.

Linkage group 7.

dl	delicate.
c ²	crumpled-2.

Linkage group 8.

p	pear.
f ¹	fasciated-1.
f ²	fasciated-2.
B ²	Blown-2.

Linkage group 9.

dp	uplicated.
st	striped.
Dil	Dilute.
w ² a	white-2a.
dg	dragonfly.
e	extended.

Linkage group 10.

r	retracted.
fo	foliate.

Linkage group undetermined.

pr	purple.
cs	criss cross.
lt ²	light-2.
iv	ivory.
Ln	Lined.
sa	striated.

Lathyrus odoratus. (Punnett, 1927.)

Linkage group 1.

A ₁ a ₁	Purple—red flower colour.
A ₂ a ₂	Long—round pollen.
A ₃ a ₃	Erect—hood flower shape.

Lathyrus odoratus—continued.

Linkage group 2.

- B_1b_1 Dark—light axil.
 B_2b_2 Fertile—sterile anthers.
 B_3b_3 Normal—cretin flower.

Linkage group 3.

- D_1d_1 Tendril—acacia leaf.
 D_2d_2 Bright—dull flower colour.
 D_3d_3 Self—flake flower pattern.
 D_4d_4 Hairy—glabrous.
 D_5d_5 Deep—picotee flower shade.

Linkage group 4.

- Ee Tall—dwarf (cupid).

Linkage group 5.

- F_1f_1 Colour—R—white.
 F_2f_2 Procumbent—erect (bush) habit.
 F_3f_3 Self-marbled flower pattern.

Linkage group 6.

- G_1g_1 Colour—C—white.
 G_2g_2 Purple—copper flower colour.
 G_3g_3 Full—dilute (mauve) flower shade.

Linkage group 7.

- Hh Clamped—open (Spencer) keel.

Table of Linkage Values in Plants.

Maize.

Linkage group 1.

	Cross-over percentage.	
$C-Wx$	21.7	(Hutchison, 1922).
$C-Wx$	17.9–25.9	(Stadler, 1926).
$C-sh$	female 2.3, male 3.4	(Stadler, 1926).
$C-pk$	2.0	(Eyster, 1924 a).

Maize—continued.

C-v ₁	30.0	(Demerec, 1924 b).
Yg-C	20.5	(Jenkins, 1927).
Yg-wx	42.4	(Jenkins, 1927).
g-sh	21-32.6	(Jenkins, 1927).
C-v ₁₅	12.5	(Phipps, 1929).
I-sh	3.6	(Hutchison, 1922).
I-wx	26.6	(Hutchison, 1922).
pk-sh	10-16.4	(Eyster, 1924 a).
sh-w ₁₁	22.3	(Demerec, 1926 a).
v ₁ -wx	7.0	(Demerec, 1924 b).
d ₃ -sh	22.9	(Demerec, 1924 b).
v ₁₅ -sh	20.0	(Phipps, 1929).
v ₁₅ -wx	19.0	(Phipps, 1929).
ms ₂ -sh	22.2	(Eyster, 1931 a).

Linkage group 2.

1 ₄ -w ₂	36.4	(Jenkins and Bell, 1930).
1 ₄ -R	36.0	(Jenkins and Bell, 1930).
1 ₄ -L ₂	43.0	(Jenkins and Bell, 1930).
R-g ₁	23.0	(Lindstrom, 1918).
R-l ₁	1.6	(Lindstrom, 1918).
1 ₁ -g ₁	19.0	(Lindstrom, 1918).
R-l ₂	33.9-35.4	(Lindstrom, 1918).
R-pg ₁	23.3	(Brunson, 1924).
pg ₁ -li	44.6	(Brunson, 1924).
R-gm ₂	31.0	(Demerec, 1926 a).
R-w ₂	17.0	(Stroman, 1924).
li-w ₂	22.0	(Stroman, 1924).
R-v ₁₈	20.0	(Phipps, 1929).
R-v ₂₀	12.5	(Phipps, 1929).
R-vc	37.0	(Phipps, 1929).

Linkage group 3.

su-Tu	28.6-29.6	(Eyster, 1922).
su-v ₈	32.4	(Demerec, 1926 a).
su-de	3.2	(Wentz, 1924).

Maize—continued.

su-wl	25.0	(Stroman, 1924).
su-de ₁	38.5	(Mangelsdorf, 1926).
su-de ₆	26.0	(Mangelsdorf, 1926).
su-ge ₁	40.0	(Mangelsdorf, 1926).
su-w ₁	20-22	(Carver, 1927).

Linkage group 4.

Te-B	20.8	(Emerson, 1920).
Te-lg	45.8	(Emerson, 1920).
B-lg	30.32	(Emerson, 1921 b).
B-sk	10.5	(Jones, 1925).
B-v ₄	16.8	(Demerec, 1924 b).
lg-v ₄	43.2	(Demerec, 1924 b).

Linkage group 5.

y ₁ -Pl	29.7	(Anderson, 1924).
y ₁ -sm	36.8	(Anderson, 1924).
Pl-sm	10.0	(Anderson, 1924).
Pl-w ₁	25.0	(Stroman, 1924).
y ₁ -m ₁	33.0	(Stroman, 1924).
m ₁ -m ₂	33.0	(Stroman, 1924).
y ₁ -w ₁	42.0	(Stroman, 1924).
y ₁ -w ₁	35.0	(Lindstrom, 1924).
y ₁ -w ₅	24.3	(Demerec, 1923).
y ₁ -w ₆	24.5	(Demerec, 1923).
w ₅ -w ₆	36.9	(Demerec, 1923).
y ₁ -v ₆	23.0	(Carver, 1927).
y ₁ -v ₇	28.0	(Carver, 1927).
v ₆ -v ₇	42.0	(Carver, 1927).
y ₁ -ms ₁	4.2	(Singleton and Jones, 1930).

Linkage group 6.

ts ₂ -P	1.0	(Anderson and Emerson, 1923).
P-f	35.0	(Anderson and Emerson, 1923).
P-br	35.5-38.0	(Kempton, 1922).
ad-br	16.8-30.0	(Kempton, 1922).

Maize—continued.

Linkage group 7.

ra-Bn	38.2	(Kvakan, 1924).
Bn-gl	18.7-29.4	(Kvakan, 1924).
Bn-v ₅	24.9	(Kvakan, 1924).
gl-v ₅	6.2	(Kvakan, 1924).
Bn-pg ₃	4.5	(Demerec, 1925).
pg ₃ -Bn	4.5	(Eyster, 1925).

Linkage group 8.

vp ₂ -pr	30.0	(Eyster, 1931 d).
pr-bv	21.7	(Li, 1931).
bv-v ₃	23.0	(Li, 1931).
cr-ms ₃	30.0	(Eyster, 1931 c).
Re ₁ -vp ₂	15.5	(Eyster, 1931 d).
Re ₂ -vp ₂	1.21	(Eyster, 1931 d).

Linkage group 9.

a ₁ -ts ₄	44.8	(Phipps, 1928).
rg-d ₁	11.9	(Brink and Senn, 1931).
ts ₄ -rg	1.7	(Brink and Senn, 1931).
rg-a ₁	41.9	(Brink and Senn, 1931).
pg ₂ -d ₁	32.0	(Eyster, 1925 : Demerec, 1925).
ba ₁ -a ₁	31.0	(Hofmeyr ex Brink and Senn, 1931).
ba ₁ -na	11.0	(Hofmeyr ex Brink and Senn, 1931).
ba ₁ -d ₁	33.0	(Hofmeyr ex Brink and Senn, 1931).
na-a ₁	35.0	(Li ex Brink and Senn, 1931).
cr-d ₁	18.0	(Emerson ex Brink and Senn, 1931).

Pisum sativum.

Linkage group 1.

		Female.	Male.	
St-B	Stipules-Salmon	30.8	33.9	(de Winton, 1928).
B-V	Salmon-Purple pod	35.4	34.5	(de Winton, 1928).
St-V	Stipules-Purple pod	6.9	4.7	(de Winton, 1928).

Pisum sativum—continued.

Linkage group 2.

Gp-I Green pod—Yellow 3.9 (male and (de Winton, unpub.,
cotyledons. female). and Sverdrup, 1927).

Linkage group 3.

R-Tl Round—tendril 1.5 (Vilmorin and Bateson, 1911,
Pellew, 1913).

R-Bt Round—Blunt 1.5 (Kappert, 1925, and Wellensiek,
pod 1925 a, b).

Linkage group 4.

K-W Keel—Glaucous 20— (Pellew and Sverdrup, 1923, and
31.14 Sverdrup, 1927).

Linkage group 5.

L-N 5.0 (Hoshino, 1915, and Pellew, 1928).

C-L 6.2-7.7-12.5 (Hoshino, 1915, and Pellew, 1928).

C-N 11.8 (Hoshino, 1915, and Pellew, 1928).

Several other linkages are reported (see Wellensiek, 1925 a, b), but there is considerable disagreement among the authorities.

Antirrhinum majus.

Linkage group 1.

aurea-marmorata 18.3 (Schick, 1930).

Perl-gran 30.6 (Schick, 1930).

aur-perl 46.5 (Schick, 1930).

Linkage group 2.

uni-ros (Baur, 1911).

ros-pal 20 ± (Baur, 1911).

(Note.—Schick and Kuckuck, 1929, give a list of factors with descriptions).

Lathyrus odoratus (see Punnett, 1925).

Linkage group 1.

A₁-A₂ 12.0

A₁-A₃ 1.0

Lathyrus odoratus—continued.

Linkage group 2.

B_1-B_2	25
B_1-B_3	6.0

Linkage group 4.

D_1-D_2	close.
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Linkage group 6.

F_3-F_2	25.0
F_1-F_2	25.0

Linkage group 7.

G_1-G_2	25.0
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Pharbitis Nil (ex Imai, 1931 a, b).

Variegated linkage group.

$v-c_1$	14.9
c_1-B_1	17.8
$v-B_1$	30.8
$v-f_3$	20-25
$v-fd$	31.0
$v-cu$	37.7

Cordate linkage group.

$co-fe$	1.2
$fe-sc$	17.7
$pc-co$	24.6
$pl-cp$	34.6
$pc-pl$	31.3
$pc-cp$	38.8

Yellow linkage group.

$y-dy$	1.0
$lt, y, \text{ and } dy$	very close.
$spr-y$	28.5
$spr-de$	15.0

Pharbitis Nil—continued.

Acuminate linkage group.

ac-Mr₂ 0.5

ac-mg 21.2

Contracted linkage group.

Ry cr ig sh ct Mr₁ Ex fl tw i Mr-r (order and locus).
0 1.2 10.3 10.3 15.9 16.9 16.9 16.9 21.9 46.5 46.5.

Speckled linkage group.

sp-w₁ 0.8

W₁-Mrf 20 ±

Delicate linkage group.

dl-c₂ 5.0

Pear linkage group.

p-f₁ 2.5

f₁-f₂ 20-25

p-B₂ 23.5

Duplicated linkage group.

dp-st 13.7

dp-D 25.6

st-D 10.1

D-w₂a less than 1.4

w₂a-dg 23.3

dg-e 30.3

(order dp st D w₂a dg e)

Retracted linkage group.

r-fo close.

Tomato.

Linkage group 1.

dwarf-peach	3.4	} (MacArthur, 1928). (MacArthur, 1926). (Crane, 1915). (Lindstrom, 1925). (Sansome, unpub.).
dwarf-oval	11.4	
dwarf-compound	28.3	
peach-oval	8.57	
peach-compound	24.46	
oval-compound	20.0	

Tomato—continued.

Linkage group 2.

lutescent-uniform 26.0 (MacArthur, 1928).

Linkage Group 3.

fasciated-anthocyaninless 14.0 (MacArthur, 1928).

Papaver Rhoeas.

Linkage group 1.

P-T Acidity-Tingeing coupling 9.2 (Philp, unpub.).
repulsion 18.0, 19.9, 20, 28.

P-F Acidity-Flushing coupling 8.6, 16.0, 22.5, 22.6.

Linkage group 2.

B-W Coloured blotch-White-edge 0.35, 0.76, 1.3, 2.0, 5.2.
repulsion

Oryza sativa.

Linkage group 1.

Ty-G1 16.59 (Chao, 1928).

ap₄-G1 22.34 „

ls₁-G1 19.43 „

Linkage group 2.

g₂-sp 1.11 „

Linkage group 3.

sa₂-ls₂ 9.8 „

In several cases preliminary maps of the chromosomes of maize can be constructed from this data, but it is less satisfactory than the genetical mapping of the four chromosomes of *Drosophila melanogaster* which is illustrated in Fig. 22. The proportion of factors identified per chromosome is sufficiently high in *Drosophila melanogaster* to make analysis by linkage profitable.

Isolated linkages between not more than two factors in various species such as *Antirrhinum* have been omitted from the list of plant linkage values (Schick, 1930), *Brassica* (see Malinowski, 1929),

Soya Bean (Owen, 1927), *Lupinus*, *Matthiola*, etc., etc. (see Matsuura, 1929).

Workers on *Pisum sativum* are in considerable disagreement upon the linkage of factors in that species. This is possibly due to the fact that different workers have been studying races which differed in the structure of the chromosomes (see p. 90). In the list only those linkages which are supported by more than one worker are mentioned.

Let us suppose that there are two pairs of allelomorphs $Aa Bb$ on the chromosomes of a bivalent. Without segmental interchange there will be no recombination between A and B , but four gametes of the constitution $2AB, 2ab$ will result from the bivalent if the dominants were on the maternal and the recessives on the paternal chromosomes or *vice versa*. To give a gametic output of $1AB:1Ab:1aB:1ab$ from such an example, two of the chromatids must have interchanged and two must not have interchanged, *i.e.*, there must have been one chiasma formed between the loci of A and of B .

Such a ratio of gametes ($1:1:1:1$) is found when there is 50% or more crossing over between the factors situated on the same bivalent. Similarly the frequency of chiasma formation between the two loci equals one. In normal cases (*i.e.*, without genetical control of chiasma formation) an average of one chiasma corresponds with 50% crossing over. With the proviso made earlier regarding genetical control it is therefore improbable that any linkage group will be found to be shorter than 50 units of crossing over. Brink and Cooper (1931) give the minimum lengths of nine maize linkage groups as

c shwx linkage group, 95 units				
r g ₁	"	"	90	"
su Tu	"	"	100	"
b lg	"	"	110	"
Y Pl	"	"	70	"
ra gl ₁	"	"	120	"
P br	"	"	120	"
pr v ₂	"	"	110	"
a ₁ ts ₄	"	"	160	"

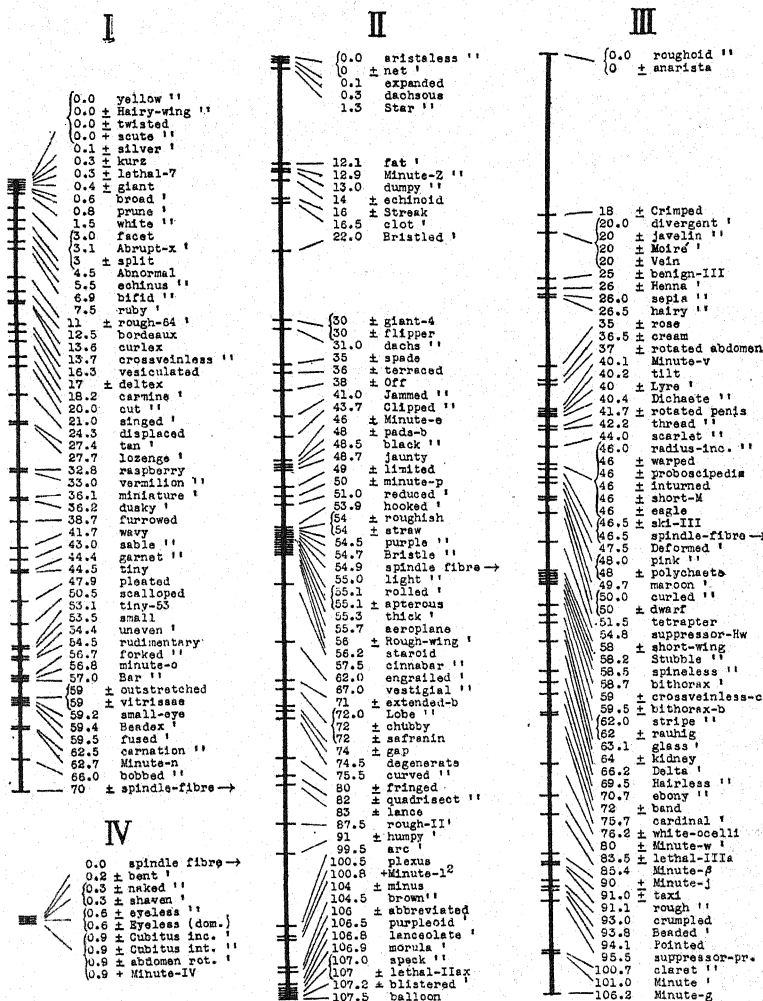


FIG. 22.—Maps constructed from data kindly provided by Dr. C. B. Bridges (June, 1932), showing principal loci in chromosomes I, II, III, and IV in *Drosophila melanogaster*. The symbol '' designates the most useful types, ' those nearly as good, while those unmarked are important only in special connections.

Chromosomes I, II and III of *Drosophila melanogaster* are 70, 106 and 107 units in length, while the fourth chromosome has 3-4 factors between which there is little crossing over. The last chromosome therefore behaves in a peculiar fashion. The graph (Fig. 21) comparing the chromosome length and chiasma formation in *Stenobothrus parallelus* and the genetic units per chromosome length of *Drosophila melanogaster* is of informative value. Here it will be seen that the X chromosome with 70 units is beginning to show the effect of genetic control. The fourth chromosome may be shorter than 50 units, but chiasma formation is probably under the influence of genetic control, and is of a specialised type (cf. Darlington, 1932 b).

It is known that crossing over does not take place in the male *Drosophila melanogaster*. Chromosome pairing takes place normally. On the chiasmatype theory the logical conclusion from the latter fact is that crossing over should take place. There is some evidence, however, which indicates that the chiasmata are localised near the attachment constriction (in the male sex) as in *Fritillaria meleagris*. This may result from some form of genetic control. Crossing over will not therefore occur in regions of the chromosomes distal to the attachment constriction if chiasmata are confined to that point.

DOUBLE CROSSING-OVER

Genetical Data. If the distance between two factors is great there is obviously a chance for two cross-overs to take place between them. This double crossing-over or coincidence is therefore a function of the distance between the factors. The distance at which double crossing-over can occur has a particular value which varies with the part of the chromosome involved. This fact was discovered genetically and the usage of the terms is genetical.

If coincidence of crossing-over involving only two chromatids takes place at x and y (in the Figures 17 and 23) the resulting crossed-over chromatids will be aBc and AbC. Hence double crossing over leaves A and C and ac in the same relation after meiosis as before. Therefore, in genetical results the detectable cross-over value between A and C will be less than the real value. Thus in calculating the cross-over value of AC from the sum of the cross-over values of

AB and BC correction must be made for this fact of double crossing-over.

As Haldane (1918 *a, b*) points out, if AB has the cross-over value m and BC has the value n in a triple heterozygote the total result of cross-overs in the different regions is :—

$$\begin{aligned} \text{non cross-overs} & \quad ABC\ abc\ (1 - m)(1 - n) \\ \text{single cross-overs} & \quad aBC\ Abc\ m(1 - n) \\ & \quad \text{,,} \quad \text{,,} \quad ABc\ aBc\ n(1 - m) \\ \text{double cross-overs} & \quad aBc\ AbC\ mn \end{aligned}$$

The value AC will be $m(1 - n) + n(1 - m)$, i.e., $m + n - 2mn$, when double cross-overs occur and $m + n$ when no double cross-

			ABC abc	aBC Abc	ABc abC	aBc AbC _u	
Species.	Factors.	Number of Plants.	Parental Combina- tions.	Recombinations (single).		Double Recom- binations.	Co- incidence.
				Region 1.	Region 2.		
<i>Primula sinensis</i> Gregory, de Winton and Bateson, 1923	SBG ♀ SBG ♂ SBL ♀ SBL ♂ BGL ♀ BGL ♂ C sh wx	2,970 2,921 641 1,312 873 1,607 12,790	1,937 1,641 366 727 553 1,006 9,741	150 256 451 107 291 574 489	829 919 210 431 23 20 2,549	54 105 20 47 6 7 11	1.13 1.21 1.29 1.19 0.61 0.7 0.11
<i>Zea Mays</i> Hutchison, 1922							
<i>Pisum sativum</i> de Winton, 1928.	BS ♀	491	312	28	146	5	0.6

Table 9. Coincidence values. Under the heading single recombinations—region 1 gives the number of cross-over plants resulting from crossing over between the central factor and the factor on the left hand, and region 2, between the central factor and the factor on the right hand.

overs occur. The value $m + n - 2mn$, however, is rarely realised in experiments. More usually the value lies between $m + n - mn$ and $m + n - 2mn$ in moderately large distances between A and C. One cross-over interferes with the formation of another cross-over

within a certain distance from it. This interference necessarily reduces the number of double cross-overs. Hence interference is the reciprocal of coincidence which is measured by the coefficient observed/calculated double cross-overs. When the coincidence is 1, interference is at a minimum, while coincidence equal to zero indicates 100% interference.

The coefficient of coincidence is most easily calculated from the formula :—

$$\text{coefficient of coincidence} = \frac{xn}{ab}$$

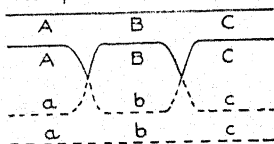
in which x is the number of observed double cross-overs, n is the total number of plants and a and b the single cross-overs observed in regions 1 and 2 respectively, i.e.,

$$\overbrace{A_1 B_2 C}$$

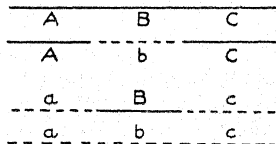
Table 9 is the result of collating the cases of three point experiments in plants known to us. It will be observed that the coefficient of coincidence in maize is less than 0.1, while in *Primula sinensis* the coefficient is high. This may be due to the large distance between SB and GL, or there may be a significant difference between the cross-overs in maize and *Primula*. The example from *Pisum* has too few numbers to be statistically significant. The data from *Drosophila melanogaster* are considerable and important in this connection. Since the chromosomes have been mapped by identifying factors at small distances from one another we can follow the process of genetical crossing over along the whole length of the chromosomes.

When the X chromosome is considered, we find on the whole that double cross-overs do not occur if the distance corresponds to less than 15% (coefficient of coincidence 0.000). From 15% to 40% the coefficient rises until at 40 units it indicates that double cross-overs are rather more frequent than expected. Bridges and Morgan (1923) showed that the coefficient of coincidence varied from place to place on one chromosome as well as between chromosomes of *Drosophila*. Thus in the X chromosome coincidence for a given length of map is greatest in the neighbourhood of "tan" where double cross-overs may occur within a section as small as 13 units. To the left of this

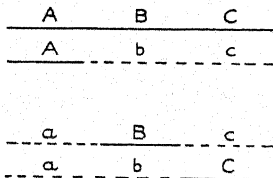
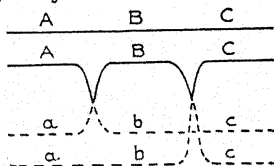
(1) Reciprocal



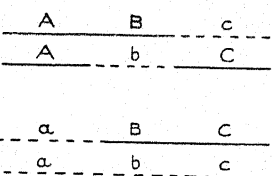
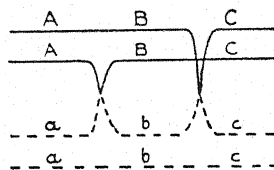
Results



(2) Diagonal



or



(3) Complementary

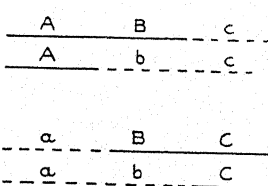
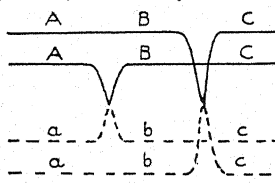


FIG. 23.—For description see text, p. 116.

region the coefficient value is lower and to the right lower still. In the second and third chromosomes the coincidences are highest near the mid points. Coincidence may be as high as 1.3 for the middle

of chromosome III and double cross-overs occur within a distance of 6 units. From these mid points the value of coincidence falls off rapidly on either side. Apparently interference is greatest at some 15 units from each end, where double cross-overs are negligibly rare in distances of 20 units (Morgan, Bridges and Sturtevant, 1925).

Cytological Basis. Consideration of the chromosome behaviour at meiosis shows that the chromatids must form two chiasmata to account for double crossing over.

Two of the four chromatids exchange material at one chiasma, therefore there are four ways in which two neighbouring chiasmata may be formed (see Fig. 23). Either the two chromatids which take part in the first chiasma are also involved at the second chiasma (reciprocal), or neither take part in the second (complementary). The other two types involve one chromatid at both chiasmata together with one of two different chromatids at each chiasma (diagonal).^{*} The reciprocal type gives gametes **ABC**, **abc**, **aBc** and **AbC**, *i.e.*, two non cross-overs and two double cross-overs. One diagonal type gives gametes **ABC**, **Abc**, **aBc**, **abC**, *i.e.*, one non cross-over, one double cross-over and two single cross-overs. The diagonal types are supplementary to one another in genetic terms, therefore the genetic output of the two diagonals will be two non cross-overs **ABC**, **abc**, two double cross-overs **AbC** and **aBc**, and four single cross-overs **Abc**, **aBC**, **ABc**, **abC**. From the complementary type of chiasma formation we expect four single cross-overs. If all four types occur with equal frequency the total output is therefore four non cross-overs, four double cross-overs, and four single cross-overs in the two regions **AB** and **BC**.

The reduction in the number of double cross-overs was originally thought to be due to the rigidity of the chromosome. It has been mentioned, however, that Haldane showed that there was interference in chiasmata formation. This alone is adequate to explain genetical interference in crossing over, if the four types of chiasmata occur with equal frequency. If there is a preponderance of one type (say reciprocal) the genetic output will be changed. This might be due to the relative position of the chromosome region

^{*} In cytological terms reciprocal and complementary chiasmata are "compensating," and diagonal are "non-compensating."

under consideration to the attachment constriction. Further data are required in order to make a fuller analysis of this behaviour which is of great importance concerning genetical segregation.

VARIATION IN LINKAGE VALUES

Variation in recombination values is of common occurrence. A difference of 2-3% crossing over is often observable between male and female gametogenesis, even on the same plant (*Pisum*, *Zea*, *Primula sinensis*). The factors S, B, G, L in *Primula sinensis* show a curious phenomenon. Although these factors are on one chromosome, the cross-over value between S and B is lower on the male side than on the female side, while the reverse is the case regarding G and L. The factors V, St, and B in *Pisum sativum* show a similar behaviour. Cf. Gregory, de Winton and Bateson (1923) and de Winton (1928).

Differences in crossing over are often found between different cultures of a species. Examples are maize, C-Wx, Collins (1924) and Stadler (1926), where crossing over ranges from 33.2% to 14.2%, and Sh-Wx 30.3-13.8%, rolled leaf in *Pharbitis Nil*, Imai (1929), and *Papaver Rhoeas*, Newton (1929), and Philp (unpub.). There is a little evidence that the variability of cross-over values is influenced by genetic as well as by environmental influences, but unfortunately the data in plants are meagre.

Usually the cross-over values from coupling and repulsion data agree closely with one another when the probable errors are kept low, and when statistically sound numbers are obtained. Demerec (1926*a*), however, found a large divergence—13.4% for coupling and 31.25% for repulsion—between Sh and C in maize. Variation in cross-over values in *Drosophila* is due to various causes, such as (1) the presence on the chromosome of linkage modifiers, *i.e.*, reducers or inhibitors of crossing-over in a particular region. These modifiers are of considerable value in the synthesis of a stock homozygous for many factors on one chromosome. For example, there is a cross-over reducer on the left end of the third chromosome of *D. melanogaster* which eliminates practically all crossing over in that region. After synthesising a race containing several factors in the left region of the third chromosome, the constitution may be retained by introducing the cross-over reducer in the homologous

chromosome. It is believed by some that the cross-over reducers may not be genetic factors but an inversion of portions of the chromosome in the region where their effect is observed. If this is indeed the case it will be seen that chiasmata formation and pairing in the inverted section and in neighbouring sections will be abnormal. (2) The age of the female influences the cross-over value. (3) Temperatures above 25° C. increase crossing-over. (4) X-ray treatment decreases or increases the rate of crossing-over. (5) Chromosome aberrations such as translocations, deficiencies, fragmentations and inversions, also influence crossing-over.

CONDITIONS OF GENETICAL CROSSING-OVER

Considerable genetical work has been directed towards discovering the stage at which crossing-over takes place. Plough (1917, 1921), and Gowen (1929) utilised the fact that temperatures over 25° C. increase crossing over in *Drosophila*. Females were raised in temperatures of 25° C. and over, and at various ages were introduced into normal temperatures for egg laying. Plough found that crossing-over had probably occurred seven to eight days before the eggs were laid, since the influence of the higher temperature upon crossing-over was still detectable up to that period. It was then concluded that crossing-over must take place in *Drosophila* early in the first maturation division. Later we shall see there is genetical evidence to show that crossing-over takes place in the prophase of the first maturation or meiotic division.

Bridges and Morgan (1919) showed that in females, temperature and age had the greatest effect on the cross-over value of loci in the middle regions of the second and third chromosomes. Stern (1926 c) showed that temperature had the greatest effect on crossing-over near the right end of the X chromosome. These regions are near the point of attachment. X-ray dosage also affects the regions nearest the attachment point more than other regions of the *Drosophila* chromosomes. Muller (1925 a), Bridges (1929).

Evidence from Triploids. The genetical results of Bridges (1916), Bridges and Anderson (1925), Morgan, L. V. (1925), Anderson (1925), and Redfield (1930), all indicate that crossing-over occurs

after the chromosomes separate into their component chromatids and before the onset of metaphase.

One method of approaching the question is to study crossing-over in triploids where the pairing is necessarily less constant than in the diploid. Bridges and Anderson (1925) working on the *X* chromosome, and Redfield (1930) on the second and third chromosomes of *D. melanogaster* raised triploids in which each of the three homologous chromosomes was identifiable by its content of factors. The history of the parts of these three chromosomes could therefore be followed in the progeny and hence the gametic output of a triplo-*X* *Drosophila* could be compared with the original input in terms of chromosome parts. It was found, for example, that one resultant chromosome was composed of parts of all three original chromosomes, indicating that after crossing-over between two of the three chromosomes at one region, a cross-over could take place at a different region between the third chromosome and one of the former participants. These *progressive* double cross-overs equal the number of *recurrent* double cross-overs in which a double cross-over only involves two chromosomes. Bridges and Anderson showed that the number of progressives was slightly in excess of recurrents on the *X* chromosome but Redfield found equal frequencies in the second and third. This rather indicates that the excess of progressives in the *X* chromosome material is not significant. The evidence is therefore that crossing-over between any two chromosomes in the triploid *Drosophila* does not interfere with crossing over with a third chromosome in a different region.

The results of the above workers have furnished conclusive evidence that (1) crossing-over takes place at the four-strand stage of prophase in the diploid and at the corresponding six-strand stage in the triploid. (2) Crossing-over may take place between any two non-identical strands at any one point. (3) Identical chromatids derived from one chromosome remain associated at the attachment constriction at anaphase of the first meiotic division. ✓

By investigating the genetical properties of triplo individuals (either triploids or trisomics) one is able to analyse in part the processes involved and to discover that there is strong agreement with the findings of recent cytological research. ✓

Evidence from Non-disjunction. Bridges (1916) experimented on non-disjunctive females of *Drosophila*. If, through an aberration in normal meiosis the two XX chromosomes of the female arrive in the same gamete instead of in separate gametes, the resulting progeny will be XXX or XXY , according as to whether the egg was fertilised by an X - or Y -containing sperm. There are two possibilities regarding the constitution of the XX chromosomes derived from the mother. Either the chromosomes XX did not pair and interchange material at the prophase of the first division, or they paired and interchanged material at prophase. The first type would only give rise to two non-disjunctive gametes of the type XYZ , xyz , where XYZ and xyz were the genetical contents of the original chromosomes. The second method would give a large range of combinations through crossing-over. Among these, Bridges found gametes containing two X chromosomes of the constitution xYZ , and xyZ . Thus gametes resulting from the second method may contain two recessive factors (xx) where the parent only contained one.

Constitution of Parental Chromosomes.	Chromatids before crossing-over.	Chromatids after crossing-over.
XYZ	XYZ XYZ	XYZ xYZ
xyz	xyz xyz	xyz xyZ

Non-disjunctive gametes might contain Xyz XYZ and xYZ xyz (for simplicity x is supposed to be situated near the attachment constriction.)

If normal disjunction took place after such crossing-over, there would be four different constitutions of the resulting gametes, viz., XYZ , xYZ , Xyz , xyz . The disjunction of the above four chromatids would be different in different sections. If the factors X and x separate from one another at the first division (reductional disjunction) the remaining factors in the above illustration will separate in an *equational* manner: $YyZz$ will go to one pole and $YyZz$ to the other. Cf. Bridges (1916), Bridges and Anderson (1925), etc. In one part of the chromatid length the genetical separation is qualitative and in another part only quantitative.

Evidently crossing-over must have occurred when the original maternal chromosome containing the recessive factor was divided

into two—that is, crossing-over must have been confined to one chromatid of each type (see diagram). Experiments with triploids and with material in which the two *X* chromosomes are attached to one another (Morgan, L. V., 1925, and Anderson, 1925) fully corroborate this view. Later data indicate more precisely the mode of segregation of the factors. Morgan, Sturtevant and Bridges (1923), Bridges and Anderson (1925), and Redfield (1930) showed that equational disjunctions did not occur throughout the length of the chromosome in triploid *Drosophila*. At one particular region from “Bar” to “bobbed” at the right end of the *X* chromosome and in the middle of chromosome III, between “scarlet” and “curled” (or “peach”), it was found that equational disjunctions were completely absent. At short distances from these points also, their frequency was smaller than expected. These regions were near the attachment constriction.

CHROMATID SEGREGATION

In the triploid there will be six chromatids, two from each of the three homologous chromosomes, which can pair with one another. If these can be associated during metaphase there are sixteen ways in which these six chromatids may be associated two at a time in the gamete. In three-fifteenths of these cases identical chromatids will be found together, *i.e.*, in 20% of cases. Redfield studied 1,106 offspring of a triplo-III *Drosophila* fly of the constitution **XXx** (**X** = dominant **x** = recessive factor). On the above hypothesis she expected 73.7 individuals $\left(i.e., \frac{1106}{15} \right)$ of each recessive type, but the numbers actually found were 6 **sc**, 6 **cu**, 13 **sr**, 16^e, 26 **ca**. Bridges and Anderson (1925) found that equational disjunctions constituted 1.1%—11.5% of the progeny instead of the expected 20%. In both cases it will be noticed that the association of chromatids is not at random, but that identical chromatids tend to stick together at one point and from that point there is a graded arrangement of frequencies from chromosome association to random association among all the homologous chromatids. That point where the identical chromatids remain together is found to be the attachment constriction.

There is therefore evidence from various experiments that the attachment to the spindle fibre is at the right end of the *X* chromosome near "bobbed," in the middle of chromosome II, and to the right of the factor purple and between the factors *sc* and *cu* in the middle of chromosome III.

A further proof that crossing over takes place between chromatids and not between chromosomes is afforded by the fact that the six chromatids of a trisome may all be different from one another after crossing-over.

Chromatids identical at the point of attachment may have parts of two different chromatids at another region. One chromatid may cross over with parts of several chromatids in different regions while the original partner may not undergo interchange.

The question arises as to whether identical chromatids may cross over between themselves. Zeleny (1921) found that reversions of Bar eye to normal eye in *Drosophila melanogaster* occurred about 1 in 1,600 times, and he discovered also a more extreme eye type—ultra-Bar double-Bar—which reverted to normal 1 in 1,700 individuals, and to Bar 1 in 2,900.

Sturtevant (1925, 1928) showed that the reversions from Bar to ultra-Bar or to normal were always accompanied by crossing-over between the neighbouring genes, forked (*f*) and fused (*fu*) and the Bar locus. He concluded that the mutations at this locus were due to unequal crossing-over. If homozygous Bar is B/B , double-Bar is BB/ϕ and normal is ϕ/ϕ , i.e., there are two Bar factors on one chromosome in double-Bar and no allelomorph in normal round-eyed individuals (see p. 153). Normal individuals were sometimes obtained from individuals homozygous for Bar and heterozygous for forked and fused ($fBfu/\phi B\phi$). Every reversion to normal eye was accompanied by detectable crossing-over between *f*, *B* and *fu*.

If another allelomorph infra-Bar (B^1) is introduced in place of *B* in one chromosome ($fB^1fu/\phi Bfu$) normal-eyed and a new type Bar-infra-Bar-eyed flies were sometimes obtained. These flies were Bar-infra-Bar and neither forked nor fused. Crossing-over had taken place in such a way that one chromosome contained B^1B and the other chromosome contained forked and fused. B^1 was inserted on the side of *B* nearest to forked at the same time as forked crossed

over. In confirmation of this it was found that BB^1/fu individuals gave rise after crossing-over to fB^1 and Bfu and never to fuB^1 . This is the normal test for the order of non-allelomorphic factors on a chromosome.

If crossing-over between identical chromatids does occur, many more apparent non-cross-overs would accompany reversions to normal eye since identical chromatid crossing-over would not be detected generally from non cross-over identical chromatids. This case, however, is abnormal, involving as it does a true chromosomal deficiency and the proof is thereby less satisfactory

Bridges and Anderson (1925), and Redfield (1929), have erroneously suggested that if identical chromatids cross over there should be an appreciable increase in detectable crossing-over between similar factors in the triploid and tetraploid as compared with the diploid.

In the diploid there are two pairs of identical chromatids and six possible ways of crossing-over, while in the triploid there are three pairs of identical chromatids and fifteen possible ways of crossing-over, and in the tetraploid eight pairs and twenty-eight possible ways. Hence, on this view identical chromatid crossing-over will constitute one third in the diploid, one fifth in the triploid and one seventh in the tetraploid of the total cross-overs. Naturally, such cross-overs will not be detectable. A ratio is therefore to be expected in detectable linkage values of two thirds in the diploid to four fifths in the triploid and six sevenths in the tetraploid; the tetraploid should exhibit 31% higher cross-over values as compared with the diploid.

There is, however, a fallacy underlying the mathematics of the argument. Darlington (1932 *a*) points out that chromosomes associate in pairs in respect of sections of the length and not all four at random as the mathematics imply. Crossing-over takes place between paired chromosomes at prophase (here the chance of crossing-over of identical chromatids is always one third), while the chromatids are assorted at random at metaphase and at the second division.

Random Chromatid Segregation. There is no cytological evidence to indicate whether identical chromatids are associated at the

attachment constriction during the heterotype division or whether any two chromatids are associated at this point. If the four chromatids of a bivalent can disjoin at random so that non-identical as well as identical chromatids may be associated during the anaphase of meiosis, the genetic consequence of this condition in a polyploid will be distinct from that where only identical chromatids are associated at the attachment constriction.

In the diploid, on the other hand, there will be no difference in the genetic results, since only one chromatid from each bivalent is included in one gamete. The first division separates the four chromatids into two pairs of chromatids, while the second division separates these pairs into single chromatids. Where there are more than four chromatids to be assorted into four gametes as in a triploid, autotetraploid, etc., it is important to know whether the chromatids assort at random or whether they are restricted in their method of disjunction. Bridges and Anderson (1925) pointed out this fact in connection with their experiments on triploid *Drosophila*, while Haldane (1930 a) and Darlington (1931 a) have shown the genetical consequences.

Blakeslee, Belling and Farnham (1923) found that a plant of *Datura* of the factorial constitution $AAAa$ (an autotetraploid) gave rise to plants of the constitution $aaaa$ when the gametic output on the random assortment of chromosomes (identical chromatids passing to the same pole) was $1 AA : 1 Aa : 0 aa$ gametes. If however the chromatids $AAAAAaa$ from the above four chromosomes are assorted at random, two at a time to each gamete, a gamete containing aa will arise once in $8! / 2! (8-2)!$ times, i.e., once in twenty-eight times. Necessarily different ratios of inheritance will be found if double reduction has taken place and these have been calculated by Haldane (1930 a).

The evidence, however, from the genetics of *Drosophila* (Bridges (1925 a), Bridges and Anderson (1925), Morgan, L. V. (1925), Redfield (1929), and others) indicates that identical chromatids are associated at the attachment constriction during the first division. Further, the experiments with *Primula sinensis* ($4x$) (de Winton and Haldane, 1931), *Dahlia variabilis* ($4x + 4x$) (Lawrence, 1929), and *Datura Stramonium* ($4x$) (Blakeslee, Belling and Farnham, 1923)

indicate that although double reduction is not frequent, it does occur, e.g., *Rubus* (see p. 215).

GENETICAL AND CYTOLOGICAL LOCI

The loci of the attachment constrictions have been determined for the three large chromosomes of *Drosophila melanogaster*. It was found that factors located within 10–15 units of the attachment constriction showed chromosome segregation, while factors at a greater distance showed ratios that approached those of chromatid segregation. The fact that there is a graded series from chromosome to chromatid ratios as the distance increases from the attachment constriction is significant. The identical chromatids were associated at the attachment constriction and all factors within a distance influenced by "interference" from crossing-over were controlled by that fact and showed chromosome segregation. As the distance from the attachment constriction increased and interference decreased, *the factors on identical chromatids were not always associated at the same pole*. Through crossing-over between non-identical chromatids *at a point between the factor and the attachment constriction* this factor had passed to the opposite pole from its homologue. When the frequency of crossing-over was sufficient the factors segregated according to random chromatid segregation.

Translocation. A striking confirmation that factors are linearly arranged on the chromosomes and of their relative position to known morphological points such as attachment constrictions and chromosome ends, is afforded by the experiments of a group of workers who utilise X-rays to increase the proportion of chromosome irregularities. Stern (1926 *b*, 1928, 1929 *a*, 1931), Muller (1928, 1930 *b*), Dobzhansky (1929, 1930 *a*, *c*, 1931 *a*, *b*) and Muller and Painter (1929).

A section of a chromosome may break off the main body of the chromosome—fragmentation. It may become attached either to a different chromosome or to a new part of the original chromosome—translocation. Exchange of material between two non-homologous chromosomes may also occur—segmental interchange. Segmental interchange can occur in various ways (see p. 264, and Darlington, 1931 *b*). Reduplication of parts of a chromosome in one nucleus

(such as a portion of the *X* chromosome translocated to III, and present in the same cell as a normal pair of *X* chromosomes and one III chromosome in *Drosophila*), or deficiency of a part of a chromosome in the nucleus may follow translocation, fragmentation or segmental interchange. These abnormalities of chromosome structure (rearrangement, reduplication and deficiency) are to be found in nature, and give rise to several interesting cases of irregular behaviour. (*Drosophila*, *Pisum*, *Datura*, *Matthiola*, *Campanula*, *Briza*, *Fritillaria*, *Tradescantia*, *Zea*, *Oenothera*, *Rhoeo*, etc.)

The abnormal condition of the chromosomes necessarily leads to certain definite genetical results which give valuable information on points which cannot be easily answered from the study of material with a more normal chromosome behaviour.

X-ray treatment increases the proportion of these abnormalities in *Drosophila*, *Datura*, and other organisms. In *Drosophila*, valuable work can be done in identifying the cytological and genetical properties of parts of a chromosome.

If a translocation takes place in *Drosophila*, the point of breakage and of reunion can be identified genetically while the size of the translocated portion may be estimated cytologically and by linkage experiments. By collecting data of a series of translocations of one chromosome, a cytological map of the position of the factors may be obtained.

Linkage studies (Anderson, 1925, etc.) had shown that a recessive factor bobbed which determined the length of hair in *Drosophila melanogaster* was situated on the *X* chromosome near the attachment constriction. Bobbed is only expressed in the female and does not appear in the male although it may be homozygous. Stern (1926 *a, b*) showed that there was an inhibitor carried by the *Y* chromosome which prevented the expression of bobbed in the male. This conclusion was based on the following grounds:—

- (1) Through primary non-disjunction, males of the formula *XO* can be obtained. If the recessive *bb* is present they show the characteristic bobbed hairs.
- (2) *XXY* females which are homozygous for bobbed do not show the bobbed character while their normal *XX* sisters do.
- (3) Gynandromorphs which have no *Y* chromosome show the

bobbed character on both the male XO and female XX sides of the body.

Experiments showed that this inhibitor was not linked to any factors on chromosomes X , II , III and IV . This supports the view that the inhibitor is on the Y chromosome. Generally, the inhibitor and bobbed were independent but Stern found that in the progeny from a cross, bobbed female $X(bb)X(bb) \times X(bb)Y^{1^{bb}}$, there were no bobbed daughters. It was found on cytological examination that the X chromosome was joined to the Y chromosome at one end—the attachment end. These non-bobbed daughters therefore had received the Y chromosome containing the inhibitor along with the X chromosome from their father. Further genetical experiments showed that the inhibitor and bb were behaving as if closely linked. It was therefore suggested that the inhibitor must have been on the longer arm of the Y chromosome which was joined to the X , and that both bb and the inhibitor were not far from the point of attachment to the spindle fibre and from each other. By further experiments, Stern (1926 *a*, 1927 *a*) showed cytologically that bobbed and the inhibitor were indeed in the regions suggested by the genetical results. Material was obtained in which, as the result of fragmentation, different lengths of the Y chromosome were present in a nucleus with the X chromosome containing bb . The expression of bb was only inhibited when the portion of the long arm of the Y chromosome nearest the spindle fibre attachment was also present. When that portion was absent and any other portion of the Y chromosome was present, the flies were bobbed.

During Stern's work it was found that both distal portions K_1 and K_2 of the Y chromosome carried material which was necessary for the fertility of the male *Drosophila*. Previously it was known that the Y chromosome did not carry identifiable factors but that it was essential for the fertility of the male. Stern's work showed cytologically that two definite portions of the Y chromosome, and not the whole chromosome, controlled fertility (see Fig. 24).

GENETICAL AND CYTOLOGICAL MAPS

Muller and Painter (1929), Painter and Muller (1929), and Dobzhansky (1929, 1930 *a*, *c*, 1931 *a*, *b*) studied the translocations of

portions of the second, third and the *X* chromosomes to other chromosomes. For example, a portion of the third chromosome may be broken off and attached to the fourth chromosome. The change in chromosome structure may be observed cytologically and the effect can be studied genetically.

From X-rayed material Dobzhansky obtained flies with a translocation and with the dominant factor *Dichaete* (*D*) in the third chromosome. On crossing these flies to eyeless or bent individuals

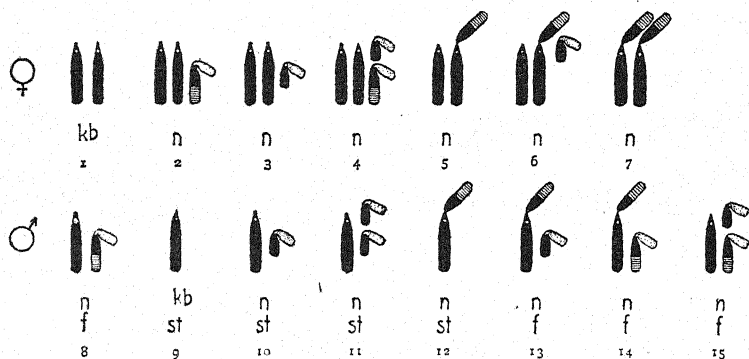


FIG. 24.—Diagram of the different combinations of the *X* and *Y* chromosomes in *Drosophila melanogaster*. The black rods represent the *X* chromosomes, and the white spot represents the point of spindle fibre attachment. The three different parts of the *Y* chromosomes are shown as follows: K_1 is cross-hatched, K_2 is dotted, and the portion carrying the bobbed inhibitor is black. In all cases the *X* chromosome carried bobbed *bb*. *kb* = bobbed phenotype, *n* = normal phenotype, *f* = fertile male, and *st* = sterile male. (Bělár, 1928.)

(eyeless (*ey*) and bent (*bt*) are recessive factors located in the fourth chromosome) he found that *Dichaete* and eyeless were linked instead of being independent. In the males the linkage was complete, but some crossing-over between *Dichaete* and eyeless was observed in the females.

It will be seen in Table 10 that in different translocations of parts of the third chromosome to the fourth, the cross-over percentages between *D* and *ey* are different, ranging from 40.7% in translocation *d* to 0.2% in *a* and *b*. The translocations involve different lengths and portions of the third chromosome. The size of the fragment

can be observed cytologically and the position of the break localised with reference to known points such as the ends, point of attachment and constrictions.

As a result of such work upon the second and third chromosomes the linear order of the factors postulated from genetical linkage

TABLE 10

Progeny of Dichæte-flies (carrying translocations) when crossed to Eyeless

(Dobzhansky, 1930)

Translocation.	Eyeless ♀ × Dichæte ♂.					Dichæte ♀ × Eyeless ♂.				
	<i>D</i>	+	<i>D e_y</i>	<i>e_y</i>	Total.	<i>D</i>	+	<i>D e_y</i>	<i>e_y</i>	Total.
a	480	424	904	1080	2	2	915	1999
b	349	324	673	818	1	2	689	1510
c	344	303	647	1140	98	61	901	2200
d	313	415	728	540	381	434	645	2000
e	306	275	581	1240	52	58	842	2192

Bent ♀ × Dichæte ♂ (carrying translocations)

Translocation.	<i>D</i>	+	<i>D b₁</i>	<i>b₁</i>	Total.
a	286	—	—	245	531
b	320	—	—	314	634
c	250	—	—	285	535
d	209	—	—	251	460
e	261	2(?)	—	249	512

studies is fully confirmed. Where a small translocation from one end of the third chromosome is observed cytologically it is found to include only those factors believed to be located at that end. Larger translocations have progressively greater number of factors.

A cytological map may be formed by noting the size of the piece and the particular factors contained in it. Fig. 25 shows the

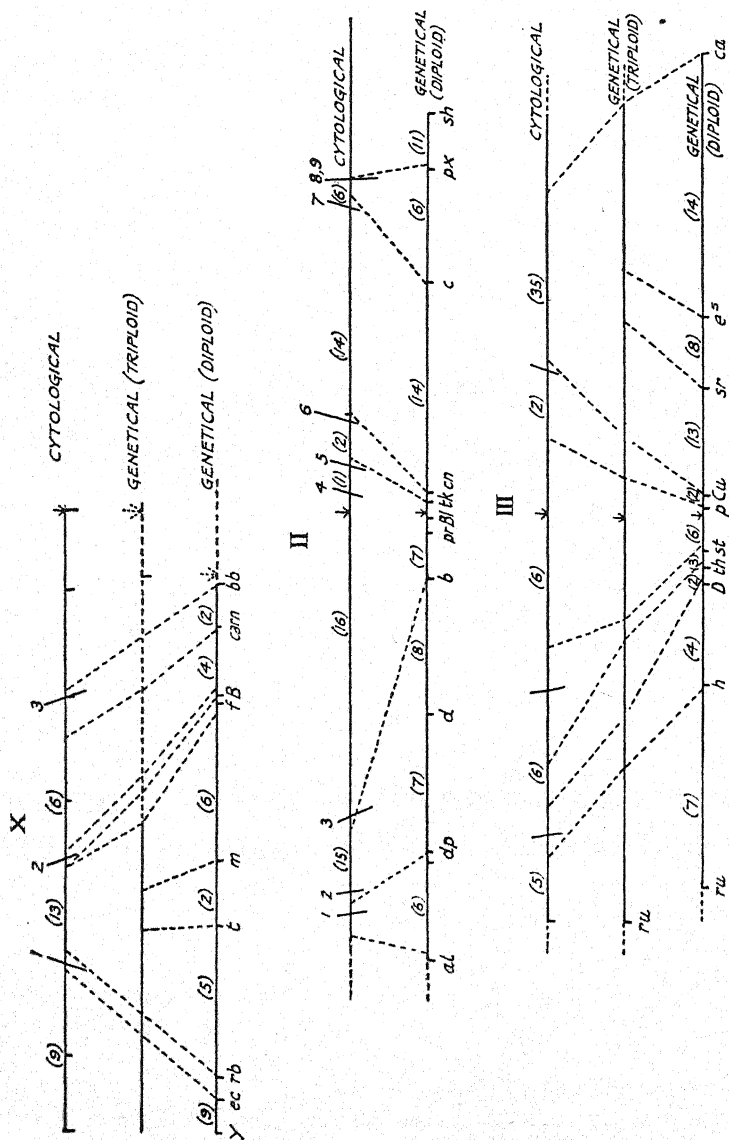


FIG. 25.

genetical and cytological maps of diploids and triploids. There is a striking difference in the relative distances of the factors between the cytological and genetical maps. In the genetical maps the distances near the point of attachment are shortened, while those in the distal regions are lengthened as compared with the cytological maps. This, of course, means that in regions near the attachment constriction the crossing-over per unit distance is much greater than in the distal regions.

The triploid genetical map is intermediate in this respect between the diploid genetical and cytological maps.

The cytological map probably gives a better representation of the physical distance between the factors. It should be remembered, however, that the chromosomes are examined at metaphase of mitosis (in the ganglia of the head), whereas crossing over occurs at

FIG. 25.—Cytological and genetical maps of chromosomes I, II and X of *Drosophila melanogaster*. Data from Dobzhansky (1929, 1930), Redfield (1929), Patterson (1931), and Morgan, Bridges and Sturtevant (1925). The figures in brackets indicate the number of known visible factor mutations in each segment. The arrow indicates the point of attachment. For factors, cf. Fig. 22. Note the differences between the genetical and cytological maps at the attachment constriction and at the distal regions.*

prophase of meiosis. If the chromosomes condense equally in all parts of their length the relative distances observed at mitosis are true representations.

The effect of translocation upon crossing over in the broken chromosome is of importance. It is found that when a breakage occurs to the right of the factor for purple on the second chromosome the crossing over in all regions to the right is decreased, but to the left it is normal. Similarly, if the breakage occurs to the left of purple the crossing over in all regions to the left is decreased, while to the right of purple the cross-over values are equal to or slightly above normal. The same phenomenon is observed in the third chromosome. The factor scarlet in the latter case is nearest the point at which the change in the cross-over value due to the effect of translocation takes place. The factor purple and the factor

* Since going to press further information has been kindly supplied by Drs. C. B. Bridges and T. Dobzhansky. The number of known genes is increased (see Fig. 22), and the spindle fibre is located nearer bb.

scarlet are situated near the points of attachment in the second and third chromosomes respectively. The following table by Dobzhansky (1929 a) illustrates the abrupt change in cross-over values as compared

TABLE II

The Standard Values of crossing-over between the Genes of the third Chromosome, and the differences between Standard Values and Values observed in the Strains carrying Translocations

(Dobzhansky, 1929 a)

Intervals.	Standard values.	Translocation strains.				
		a.	b.	c.	d.	e.
<i>ru—h</i>	23·8	— 6·6	— 2·6	+ 3·1	+ 5·2	— 4·3
<i>h—D</i>	13·6	— 10·7	— 7·7	+ 1·8	+ 1·3	— 2·0
<i>D—th</i>	1·1	— 0·9	— 0·9	+ 0·4	0·0	+ 0·1
<i>th—st</i>	0·8	— 0·6	— 0·5	+ 0·1	+ 0·1	— 0·3
<i>st—cu</i>	8·1	— 1·5	— 3·4	— 3·6	— 2·2	— 3·0
<i>cu—sv</i>	15·4	+ 1·2	+ 1·7	— 11·7	— 2·8	+ 0·3
<i>sv—e^s</i>	10·3	+ 1·4	+ 0·3	— 2·8	— 1·4	+ 1·3
<i>e^s—ca</i>	31·0	0·0	+ 0·1	— 2·1	— 11·8	0·0

with normal in the different translocations. Translocations a, b and c involve one side of the third chromosome, while c and d involve the other arm.

A reasonable explanation of this phenomenon may be put forward in terms of the chiasmatype theory. If homologous chromomeres pair, one expects that the whole chromosomes will only pair normally if the linear arrangement of these homologous chromomeres is the same in both chromosomes. This order will be upset by translocation, inversion or duplication, and both the part affected and neighbouring portions of the chromosome will behave abnormally. Hence chiasma formation and crossing-over will be influenced greatly by the presence of non-homologous segments in apposition to one another on the pairing chromosomes.

Dobzhansky (1931 a) arrives at a very similar conclusion from genetical lines of approach.

LINKAGE GROUPS AND CHROMOSOME NUMBER

A consequence of the chromosome theory is that the number of linkage groups should equal the number of non-homologous chromosomes in the haploid set. The *Drosophila* genus gives evidence that this is the case. *D. melanogaster* has four chromosomes and four linkage groups, *D. virilis* has six chromosomes and six groups, *D. obscura* has five chromosomes and five groups, and *D. Willistonii* has three chromosomes and three groups. Other *Drosophila* species have fewer groups than chromosomes due to the small number of known factors.

An interesting case is described by Muller (1930 *a*) and Muller and Painter (1929) in *Drosophila melanogaster*. A fly known as "tubby" has a shortened body and bulgy eyes. The factor for tubbyness was found to be independent of any factors on the four chromosomes and behaved as if constituting a linkage group of its own. Cytological examination showed that the tubby flies had a fragment of a chromosome as well as a normal complement. Unfortunately the chromosome from which the fragment was derived is unknown.

The genetic data in plants are generally insufficient to give evidence concerning the relation of number of linkage groups and number of chromosomes. The proportion of known factors to number of chromosomes is too low. Whether the factors of maize, *Primula sinensis* or *Pharbitis*, for example, fall into ten, twelve or fifteen groups respectively, cannot be settled until more factors are known, since cross-over percentages of 50% and over cannot be distinguished genetically from independence in a diploid.

There are seven linkage groups in *Lathyrus odoratus* and seven chromosomes in the haploid set.

One would expect that the genetical work in *Pisum* carried on since the time of Mendel would indicate whether or not there are seven groups of linked factors corresponding to the seven chromosomes. The presence of segmental interchange and possibly trisomics, however (Håkansson, 1929 *b*, 1932 Richardson, 1929, and Pellew and Sansome, 1931), will naturally complicate the genetical experiments.

Emerson (1921-1924) found that in seeds of maize heterozygous for **Cc**, a basic factor for colour and **Wxwx** a factor for starchy endosperm, sports of colourless aleurone in a normal coloured aleurone were sometimes seen and these were underlaid by waxy endosperm in the majority of cases. When heterozygous for another colour factor **Aa** along with **Wxwx**, however, the simultaneous change in aleurone colour and endosperm characters did not take place. **C WxSh** and **I** are factors all on one chromosome (Stadler, 1930, and Emerson, 1924 a). Emerson found 121 out of 127 mosaic seeds in which a change in one of the characters determined by one of these factors was accompanied by a change in the remaining characters that were segregating. For example, **cwxsh** × **CWxSh** normally gives a seed with endosperm **ccCwxwxWxshshSh** completely dominant for colour, starchy and normal endosperm. Two such seeds had a section of colourless aleurone which was accompanied by **wx** and **sh** endosperm. The aberrant endosperm part is apparently due to the falling out of the chromosome bearing **CWxSh**.

If the two factors are on different chromosomes no correlation should be observed in their "mutation." Genetical work has shown that the chromosome bearing **C** is not homologous with that bearing **Su**. Of 41 mosaic seeds whose normal part was **CSu** in type, 14 had an aberrant part **su** accompanied by **C** and 27 had **Su** accompanied by one or more of the recessives **cwxsh**. Emerson points out that analysis of aberrant endosperm seeds of maize gives valuable evidence of independence or linkage of factors and by this method has established that the **C**, **Su**, **Y**, **R**, **A** linkage groups are distinct, except for the relationship of **R** to **A**, which cannot be tested since **R** must be present for **A** to show segregation and *vice versa*.

Stadler (1930), continuing this type of experiment, finds that in normal material the frequency of endosperm chimæras varies from 2/1,000 seeds for the chromosome carrying **Su** to 9/1,000 for the chromosome carrying **A**, while the evidence from the **Cwxsh** chromosome indicates that often only a part of the chromosome has fallen out or is deficient. X-raying of **Cwxsh** pollen causes in some cases a greater or smaller part of the chromosome to drop out. It is interesting that mature pollen carrying **A**, when irradiated, some-

times gives rise to deficiency in the endosperm or the zygote independently. This is expected from the fact that one pollen nucleus fertilises the ovum while the other fuses with the fusion nucleus of the embryo-sac. If, however, the pollen is X-rayed earlier, the pollen nucleus has not divided, and it is found that deficiencies in the zygote and endosperm are absolutely correlated.

Stadler also found that the deficient area in endosperms sometimes gave rise to "recovered" cells. Five seeds out of 2,374 resulting from *ARCwxpr* \times X-rayed *ARCWxPr* were colourless waxy (*cw \times*) except for small spots which were coloured and non-waxy (*CW \times*). This recovery of a deficient area also occurred in the plant with regard to the *A* carrying chromosome. "Recovery" is not more frequent per cell in X-rayed than in untreated material, but since more deficiencies are produced by X-raying, more recoveries are obtained. The author gives evidence that the recovered areas are not direct cell descendants of normal areas but have resulted from deficient areas. Further investigations are needed for an explanation. Randolph has shown that deficient areas in the endosperm resulting from X-raying of pollen or of embryos commonly involve the absence of a cytologically detectable chromosome fragment. Stadler puts forward evidence that the X-raying of the pollen either makes the *Cwxsh* fragment of the chromosome drop out or become inactive and recovery is due to the re-establishment of normality. He suggests that the chromosome part becomes inactive and is transmitted without true mitotic division to cell descendants. Recovery, he imagines, will accompany the resumption of full mitotic division by the fragment.

Further confirmation of the close connection between chromosomes and factors is obtained from plants with a chromosome number different from the usual diploid number. Tomatoes, *Datura*, *Matthiola* and *Nicotiana*, among other species, sometimes produce plants with $2x + 1$ chromosomes. When this occurs it is usually accompanied by a change in the character of the plant, or the accentuation of one or more characters seen in the normal diploid. In *Datura* the diploid chromosome number is 24, consisting of two sets of twelve chromosomes. Correlated with the

fact that any one of these twelve chromosomes may be present in excess in the trisomic form, twelve different character changes can be recognised. Indeed, Blakeslee and his co-workers (1924-1930) are able to identify parts of some of the twelve chromosomes with a particular phenotypic expression. This point will be dealt with further under polyploids.

CHAPTER III

THE CONSTITUTION OF THE FACTOR

Presence and Absence Hypothesis—Eyster's Genomeric Hypothesis—Mutable Genes—Step Allelomorphism—Thompson's Side-chain Hypothesis—Goldschmidt's Physiological Hypothesis—Fisher's Theory of Dominance.

Presence and Absence Hypothesis. Mendel supposed that there was one factor for each of the characters that he studied and that each allelomorph was a distinct entity. He made no attempt to discover the relationship between two allelomorphs. Mendelian workers soon turned their attention to the elucidation of the nature of the factor and the relationship of the allelomorphs.

One of the first theories suggested was the presence and absence theory of Bateson and Punnett (Bateson, 1930). At the first enunciation, it was supposed that an organism which exhibited a dominant character, possessed a factor which was absent in the organism exhibiting the recessive and alternative character.

Later it was found that more than one factor could be allelomorphic to a dominant factor. For example, there is a multiple allelomorphic series controlling the size of the eye of the flower of *Primula sinensis*. There are three factors all allelomorphic to one another. The factor Q for normal eye is dominant to a factor q for large eye, called Primrose Queen, after the variety in which it appeared, and both Q and q are recessive to Q_1 a factor for no eye (Queen Alexandra). When Primrose Queen (qq) is crossed to normal-eyed plants, the F_2 segregates into 3 normal : 1 Primrose Queen in respect to eye type. The cross, Queen Alexandra \times Primrose Queen, segregates in F_2 in the ratio 1 Queen Alexandra : 2 with intermediate eyes similar to the F_1 (Q_1q) : 1 Primrose Queen. There is no appearance of normal eyes as would be expected if normal were in a different locus. The third cross, normal \times Queen Alexandra, segregates in the ratio 1 Queen Alexandra : 2 intermediate eyes Q_1Q : 1 normal with no Primrose Queen eyes appearing.

Johannsen (1923) and Morgan (1919) suggested that the theory of presence and absence was upset by the occurrence of more than two allelomorphs at one locus. Morgan pointed out in his argument that there could not be two absences corresponding to one presence. As Bateson (1926) points out, however, this assumes that the recessive contains no factor at all to correspond with the presence of one in the dominant, whereas it is more probable that only a part of the dominant factor is absent in the recessive factor.

In the example quoted above, if A_1 represents the top dominant of the series (Queen Alexandra eye) which acts as an inhibitor of the eye, normal eye could be represented as $A_1 - \frac{1}{4}$ and Primrose Queen as $A_1 - \frac{1}{2}$. The figures are purely hypothetical and are obtained from the relative expression of the factors A_1 , A and a . It is not known if expression is a linear function of factor content.

Several allelomorphic series, such as that which governs the structure of the flower in *Antirrhinum majus*, or the eye-colour and wing shape in *Drosophila melanogaster*, might well be composed of factors which are similar in kind but different in quantity.

The presence and absence theory thus assumes a quantitative difference between the dominant and recessive allelomorphs. It will be seen later that several recent theories of the nature of the gene are similar in some respects. It seems necessary to assume that that there is also a qualitative difference between the dominant and recessive factors.

P. Hertwig (1926) studied the "def." series of multiple allelomorphs of *Antirrhinum*. "Def." is normal, def. chl. (chlorantha, Schick and Kuckuck) has light green flowers with under-developed upper and lower corolla lips, def. nic. (nicotianoides, Schick and Kuckuck) has a very short corolla and petaloid stamens while the extreme def. gli. (globifera, Schick and Kuckuck) has much reduced floral parts and deformed gynoecium with sometimes as many as six styles.

The series in order of dominance is, normal-chlorantha-nicotianoides-globifera, with normal completely dominant over all the others. The heterozygote chlor.-nic. is similar to chlorantha, but can be distinguished from it. Chlor.-gli. is intermediate between chlorantha and globifera, while nic.-gli. is closer to nicotianoides than to globifera. In this series, both dominance of one factor over

another with respect to the principal character expression and the graded increase in abnormality, as we pass down the series, might well be obtained from a quantitative difference between the factors.

Agol (1931) has pointed out that the series of factors controlling wing shape in *Drosophila melanogaster*, namely, normal, nick, antlered, strap and vestigial, might also be regarded as differing from one another on a quantitative basis. Here the homozygous nick and normal flies cannot be distinguished phenotypically, but normal is completely dominant to vestigial, whereas nick is not. Therefore the heterozygous forms (+ v) and (nick-vestigial) are distinguishable.

Among other series of multiple allelomorphs which show a graded difference in expression of characters is the triple allelomorphic series Gr, G, g in *Phaseolus* (Emerson, 1909 and Tjebbes, 1931). Here the recessive factor g gives plants with yellow pods and foliage, the top dominant Gr gives green pods and foliage, while the intermediate factor G gives yellow pods and green foliage. Again there are four factors in a multiple allelomorphic series which control the distribution of pigment in seed coat of the Soya bean (Owen, 1928 b, and Nagai and Saito, 1923).

Whether multiple allelomorphic series of factors in other plants exhibit quantitative differences in expression is as yet difficult to determine. The character which is influenced by the factors of the series may be one of structure or physiology. Until the train of actions between the factor, as origin, and the character expression, as product, is more fully known, it is unwise to speculate as to the differences between the nature of the factors on the basis of differences between the expressions of two factors.

Imai (1931 a, b) enumerates seven different series of multiple allelomorphs in *Pharbitis Nil*. The factors in each series are arranged below in the order of dominance.

- (1) Normal, maple, willow (shape of cotyledon and leaf, split flower).
- (2) Normal, smeary, faded (flower pattern).
- (3) Normal, contracted, star (contraction of organs, flower shape).
- (4) Normal, yellow inconstant, yellow (foliage colour).
- (5) Normal, crepe, reversed (constitution of leaf).
- (6) Margin reduced, normal, margin slight (margin of corolla).

- (7) Normal, feathered, creased (crumpling of leaf and feathering of corolla).

In *Pisum sativum* Tedin (1925) indicates that in the presence of **A**, a factor for flower colour, leaf axil spot is controlled by three factors, **Dw**, **D** and **d**. **DwA** gives a double ring, **DA** a single ring, and **dA** and all **D** factors with **a** give no ring of colour in the leaf axil.

Both in maize and *Drosophila* multiple allelomorphic series with many members are known. Emerson (1914, 1917, 1918, 1921 *b*), in maize, for example, found that the factor **R**, which is one of the complementary factors for plant, pericarp, and aleurone colours, was

TABLE 12
Anderson (1924)

Factors.	Pericarp colour.	Cob colour.
<i>RR</i>	red	red
<i>OR</i>	light red to orange	red to orange
<i>WR</i>	white to pale orange	red
<i>OW</i>	light orange	white
<i>CW</i>	red or orange, white capped	white
<i>CR</i>	red or orange, white capped	red
<i>WW</i>	white	white
<i>VV</i>	variegated	variegated
<i>MO</i>	variegated, crown patch	light to white

a member of the multiple allelomorphic series **R_n**, **R_g**, **r_n**, **r_g**, **r_{ch}**, **r_{rg}** (see p. 38), and also that the factors **B**, **B_w** and **b**, which modify the expression of certain plant colours such as sun-red formed another series.

Emerson (1917) studied several pericarp colours in maize and found that each depended on a factor which was not inherited independently, but which showed complete linkage. These were further studied by Anderson and Emerson (1923) and Anderson (1924), who found that they formed a multiple allelomorphic series. Table 12 illustrates the phenotypic effect of the factors. Anderson found that any factor which determined colour was dominant to factors which determined colourless pericarp, and those which gave darker colours were dominant to those determining lighter

colours. Red and variegated were completely dominant to white, but P_{or} , P_{ow} , P_{cr} and P_{cw} gave intermediate colours when combined with white, although the distribution of colour was similar to that in the coloured parent.

Anderson points out that many more factors in this series can be isolated, since subdivisions of each colour class can be made. Emerson had shown that variegated **VV** could be divided into light, medium and heavy variegation, while Hayes (1917) showed a similar series for mosaic. These mutable types are unique in that they can quickly produce a completely graded series of multiple allelomorphs.

Emerson (1914, 1917) showed that variegated pericarp in maize was due to mutations in the pericarp colour factor during the course of the plant's ontogeny, and found that changes from variegated **V** to self-colour **S** were reversible, but with different frequencies. He also showed that only one of the factors mutated at a given time in homozygous material. In heterozygous material, where colourless pericarp was present along with either **V** or **S**, the colourless pericarp factor did not mutate.

Eyster (1924 *d*, 1925) studied plants which contained the factors **ow** and **ww**, *i.e.*, they were heterozygous for orange pericarp—white cob, and white pericarp—white cob (note here that it is preferable to designate the factors thus since they have not been definitely proved to be members of the above allelomorphic series of **P** factors, although there is a strong presumption that this is the case). A complete range of colours from colourless to cherry-red pericarps was found on plants of the constitution (**ow ww**). Mutations from orange pericarp to red and to white with the consequent variegated patterns were therefore observable. If seeds with a light coloured pericarp were planted, the resultant progeny still consisted of a range from the lightest to the darkest colours. In all cases, however, the mode of the colours of the ears of the progeny approached that of the parent ear. It was found that orange seeds taken from an ear having both orange and red seeds produced plants with various shades of orange pericarp while the red seeds gave plants with red ears. The orange pericarp colour persists until late in the development and then may break up into the components

red and white. This change is the most frequent (13 per 1,000 seeds), while the change from orange to red takes place less frequently (10 in 1,000). Those with heavy variegations (where the colours are intense and in large patches) are unstable and give rise to light variegations (8 in 1,000).

The variegated colour forms which resulted from the breaking up of the orange pericarp into the constituents red and white were all heritable. As in those seeds with orange pericarp each colour form tended to reproduce itself, the mode of the colour range of the progeny from a particular ear corresponding with the type of variegation of that ear. Mosaic pattern, another of the factors in this P series, was also found to behave in a similar manner. Mosaic pattern results from the juxtaposition of red and white tissue in the pericarp.

Eyster's Genomeric Hypothesis. Another range of colours, including variegations, in *Verbena*, was reported by Eyster (1928). This formed an orthogenetic series similar to that of orange pericarp—colourless in maize. Here, however, dilute colour was dominant over more intense colour. The various series were thought by Eyster to have had a quantitative basis for their variation.

He therefore put forward the "genomeric theory" in which he supposed that each gene was made up of smaller elements or genomeres. If some of these are pigment producing and others are non-pigment producing, the intensity of colour produced will depend on the proportion of each present in the gene. The range of colours and variegations produced would result from the self propagation and random distribution of the genomeres at mitosis.

If the number of genomeres in a gene is K, a scheme can be drawn up to represent the various types. For example, a series (KC) : (K - 1C, c) : (K - 2C, 2c) (Kc), where C and c represent the colour and non-colour producing genomeres respectively, according to Eyster, will represent the constitution of the genes in such a multiple allelomorphic series as in maize pericarp colour determination. If a gene with (K - 1C, c) genomeres divides, it may form two genes identical with itself or form one (KC) and one (K - 2C, 2c). Such a change would ultimately lead to the formation of factors with all possible

numerical combinations of C and c genomeres. Necessarily, only Kc and KC genes would be stable. On this hypothesis it is expected that lighter and darker areas arising by this method will be equal in number and in size. Eyster shows that darker and lighter areas are segregated in the 1:1 ratio expected, from dilute red in association with a stable factor in maize. Dominance of one factor

TABLE 13

Mutability in Hybrids of the "def." Series of Factors in Antirrhinum majus (after Hertwig, 1926)

nic. \times $\frac{\text{nic.}}{\text{gli.}}$		nic. 171	$\frac{\text{nic.}}{\text{gli.}}$ 46	normal 124
$\frac{\text{nic.}}{\text{gli.}}$ \times $\frac{\text{nic.}}{\text{normal}}$		nic. 170	$\frac{\text{nic.}}{\text{gli.}}$ 103	normal 422
gli. \times $\frac{\text{nic.}}{\text{gli.}}$		gli. 44	$\frac{\text{nic.}}{\text{gli.}}$ 63	normal 24
$\frac{\text{nic.}}{\text{gli.}}$ \times F ₂	$\frac{\text{nic.}}{\text{gli.}}$ 77	gli. 48	nic. 64	normal 81
nic. \times $\frac{\text{chlor.}}{\text{nic.}}$		nic. 169	chlor. 165	

over another on this genomeric theory depends on the number of genomeres of a particular type present—C in maize, where colour is dominant, and c in *Verbena*, where colour is recessive.

Mutable Genes. Among the factors which are members of a multiple allelomorph series, there are several which mutate with a definite frequency to another member of the series, or to a state, which is indistinguishable from that of another allelomorph. Generally, the mutation is in the direction of the wild type allelomorph, which is commonly, but not always, the top dominant

of the series. Such mutable genes have been found in maize and Verbena and in

Antirrhinum, Baur (1924), Hertwig (1926). See Table 13.

Primula sinensis, flaking of the petals, de Winton (unpub.).

Pharbitis Nil, Imai (1931 a, b), Yellow inconstant, etc.

Delphinium, *Drosophila virilis*, Demerec; *Drosophila melanogaster*, Patterson (1930).

Three cases in *Drosophila virilis* and two in *Delphinium* have been more intensively investigated by Demerec (1927, 1928, 1931) for the discovery of the nature of mutable genes.

In *Drosophila virilis* there are genes situated at three loci which mutate from a recessive condition to the wild type or dominant. At one locus are miniature- α , β and γ , three genes which affect wing shape, at the second locus reddish- α , a gene which affects body colour, and at the third locus magenta- α , a gene which affects eye colour.

In the case of reddish- α , miniature- α and magenta- α the gene mutates to the dominant and no reverse mutation has been observed to occur during the experiments. Reddish- α is an allelomorph of yellow and of reddish-1, both of which are stable genes recessive to normal. The reddish- α gene associated in a fly with one of these allelomorphs shows reversion to the wild type gene. For example, flies with reddish- α and yellow genes give rise to reddish- α , yellow and wild type flies. This reversion is proved not to be due to chromosome aberration, unequal crossing over, nor to multiple factor inheritance but to gene mutation. The reversion frequency is variable and by inbreeding is decreased from 12.4% to zero at the seventh generation. It can, however, be kept highly variable by selection. The reversion only takes place in heterozygous flies and only at the maturation division of heterozygous females.

On the other hand, miniature- α , which is an allelomorph of the stable miniature-1 will mutate in homozygous as well as in heterozygous flies at germ cell formation and in somatic cells. Mosaics of miniature- α and normal wing characters can be found among such miniature- α flies. The frequency of mutation of one allelomorph to another may be influenced by selection. Demerec has isolated two different genes which affect the frequency of reversion. One induces a high mutability of miniature- α in somatic

cells, but does not noticeably affect the mutability of the germ cells, while the other mainly affects the rate of mutation in the germ cells.

In *Delphinium ajacis*, rose- α , which is a factor for flower colour, mutates frequently to its purple wild type allelomorph. From seed of a selfed rose- α parent, variegated plants are obtained, in addition to a few purple and a few rose variegated and purple chimærical plants.

Purple plants arise through the reversion of rose- α to purple in the germ cells. Chimærical rose purple plants are the result of somatic reversion which has occurred early in ontogeny. It is noticeable that when a purple spot occurs on a rose- α plant it consists of one or more purple cells, surrounded by distinctly lighter purple cells. This may be due to diffusion of the pigment from the mutated cells. The stock had been started with one heterozygous plant with the lilac and rose- α genes as the allelomorphs. Since only rose- α mutates, Demerec in his study virtually followed the descendants of one rose- α gene. From such a plant the number of mutations of the rose- α gene to purple was about 1,182 per 100 sq. cm. of somatic tissue. Demerec showed that the mutation rate was the same in gametogenesis and somatogenesis and remained constant through four sexual generations.

Lavender- α mutates to purple in a strikingly different manner. It has a high rate of mutation in the early stages of development of the plant and is stable, or shows little mutability, in the early stages of petal and sepal formation, with a return to high mutability in the last stages of development.

Demerec points out that the behaviour of these mutable genes is an orderly one. Reddish- α only mutates in the germ cells, miniature- α and magenta- α mutate in both somatic and germ cells, miniature- γ , another allelomorph of miniature- α , mutates only in the somatic tissue, while miniature- β does not mutate like the others to the wild type, but mutates with a low frequency to mutable miniature- α and γ .

As Demerec (1931) states, it is difficult to account for the behaviour of these mutable genes on Eyster's genomeric hypothesis. The constancy of the rate of mutation through four generations in *Delphinium* and the constancy of miniature- α in *Drosophila virilis*

under the influence of the gene which affects rate of mutation is not consistent with the view that the gene is liable to change in the proportion of genomeres at every cell division. Moreover, the constancy of the mutation rate in somatic tissue of *Delphinium* through twelve cell generations is inexplicable by mathematical means, on the genomeric hypothesis. Hence Demerec favours the view that the gene mutation is more of the nature of a chemical change than a physical assortment of gene particles.

Numerous other examples of genic mutability such as the flaking gene of *Primula sinensis*, yellow inconstant (Imai, 1929), cream (Imai, 1929) and flecked (Imai, 1931 *a, b*) in *Pharbitis Nil* agree in that the mutability rate does not vary greatly from one generation to another and that the mutation is from the recessive to the normal dominant type. The mutation rate is low, ranging from about 0.2% in *P. sinensis* flake to 3.7% in flecked *Pharbitis Nil*.

In several cases these mutable genes have stable allelomorphs whose effects cannot be distinguished phenotypically from those of the unstable genes. Examples of such genes are reddish, miniature and magenta in *Drosophila virilis*, yellow constant in *Pharbitis* and two peculiar cases reported by Imai in *Plantago* and *Celosia*. In these two latter examples, an unstable normal type mutates to the aberrant recessive, while another normal type does not mutate.

It has been found on treatment with X-rays that certain loci of *D. melanogaster* give more visible mutants than others (Muller, 1928 and Patterson, 1929, etc.). These loci, such as scute, forked, and eye colour exhibit several allelomorphs. It would appear that certain loci have more mutable genes than others at a given stage in the life history of the organism.

Sax (1931) attempts to show that the parts of chromosomes with increased crossing-over per unit distance in the *X* chromosome of *Drosophila melanogaster* contain more mutable genes than other portions. When visible mutations and the genetic map of *Drosophila* are considered together there may be a small correlation. It is necessary, however, to consider lethal mutations (Muller, 1930 *b*) and the real map distance which is probably close to that shown by the cytological map (see p. 130). When this is done (see p. 131) the correlation disappears. Nevertheless, there may be

some connection between chromosome fragmentation in the general sense and factor mutation.

Since the mutant cells and tissue are well defined from the original tissue, both in the above examples and in various mosaics produced by Muller, (1930 *b*) in *Drosophila* by means of X-rays, it is more probable that the gene does not consist of more than one or two separable parts. In *Delphinium*, Demerec finds that the rate of mutation of rose- α is the same in the cells early and late in ontogeny. This indicates that the time of mutation is limited to a definite period of mitosis which is not interkinesis. If mutation occurred before the division of the gene, at least two cells with the mutated character would always be produced. The fact that one-celled mutations were found at the rate expected, according to the laws of chance, indicates that the mutation occurred at or after the gene had divided into two.

Hedeyatullah (1931) believes that splitting of the chromosomes takes place at metaphase in the previous cell division instead of as generally supposed at early prophase of the present cell division. If gene mutation takes place at or after the splitting of the chromosomes the consequences according to each view are different. If a dominant gene mutation occurs thus, and if the mutation does not show until the chromosome is homozygous for the dominant mutation, according to the older view the mutation will first show its effect in one of the two daughter cells from the cell in which the mutation took place, while according to Hedeyatullah's view it will first show its effect in one of the four granddaughter cells.

Hertwig (1926) finds in *Antirrhinum* that globifera mutates back to normal. It can do so either in the somatic or germ cell tissue, and either in homozygous or heterozygous material. Combination of globifera with any of the other allelomorphs normal, chlorantha, nicotianoides, indicates that certain arrangements increase the rate of mutability of globifera. Table 13 illustrates the segregation of various combinations.

Step Allelomorphism. Serebrovsky (1927), Levit (1930), Dubinin (1929) and Agol (1931), put forward the view that the locus of one gene contains a group of sub-genes, arranged in a linear order and each contributing a definite characteristic to genetic determination.

Thus, the following diagram (Fig. 26) pictures the hypothesis in reference to the locus of the multiple allelomorphic series of scute in *D. melanogaster*. The different allelomorphs sc_1 , sc_2 , sc_3 and sc_4 occupy different regions of the district in the locus, and therefore the author views each of these genes as a sub-gene only partially allelomorphic to another of the same allelomorphic series.

Serebrovsky arranged the characters of bristles controlled by the scute series in a linear order of effect and showed that this order corresponded with that of the supposed position of the sub-genes in the district of the locus. Sturtevant and Schultz (1931) extended this series of characters and showed that each allelomorph had a maximum effectiveness on "definite" bristles, while their effect on other bristles fell off equally on either side. Therefore, each scute

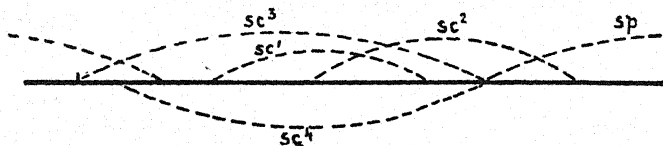


FIG. 26.—Diagram of the scute locus in *Drosophila melanogaster* based on the step allelomorphism hypothesis. (Agol, 1931.)

allelomorph has a definite effectiveness in inhibiting the development of successive bristles. It is found that sc_4 affects all the bristles, and that sc_1 , sc_2 and sc_3 each do so in part, except for the frontal dorsocentral bristle which is influenced by sc_3 and those on the wing influenced by sc_2 . If sc_4 were a partial allelomorph of these sub-genes, then in a hybrid between flies with sc_4 and those with other scute factors, only the coinciding characters determined by both sub-genes will appear, and the remaining characters will be of the dominant normal type. Agol found that this was always the case in the scute locus. For example, sc_{10} gives bristles on the head, but not on the dorsocentral region, while sc_4 gives the reverse. The

hybrid $\frac{sc_4}{sc_{10}}$ gives hairs on both regions. The Serebrovsky school believe that this indicates that sc_4 and sc_{10} occupy two different regions in the scute locus, which together fill almost the whole region of the locus. Where the phenotypic manifestations of two of the

allelomorphs are different, reversal to the dominant or normal takes place in that difference only.

Agol points out that scute₂ besides affecting the bristles, makes the wings spoonlike and wrinkled. Scute₄ does not affect the wings. The neighbouring gene to the right of scute is spoon wing. Therefore Agol suggests that scute₂ extends along the chromosome into the district of the locus spoon, but that scute₄ does not.

It is said that the scute allelomorphs are only partial allelomorphs. The position and space taken up by one sub-gene allelomorph in the district of a locus may not be the same as that of another allelomorph, but by a step arrangement a long "stair" of allelomorphs is assumed, which passes from one locus to another throughout the length of the chromosome.

A consequence of this theory is that one gene may occupy less space on the chromosome than its allelomorph, and if the genes are an integral part of the composition of the chromosome, one chromosome containing one allelomorph may be shorter than the homologue containing a different allelomorph. This might be detectable by linkage studies. Serebrovsky (1927) and Serebrovsky, Ivanova and Ferry (1929) claim to have detected this difference in length in *Drosophila*.

If allelomorphs are definite physical granules in the chromosome and crossing-over occurs as a result of the breaking of the thin twisted threads at prophase we should expect the substitution of one type of granule for another to have a certain influence on the points and the number of breakages of the chromosomes (Gowens, 1919). On the second chromosome of *D. melanogaster*, black, purple and cinnabar are genes with the loci at 47.5, 53 and 54 units of the genetic map respectively. By carefully controlled experiments Serebrovsky (1927) showed that the cross-over value between black and cinnabar was higher when the dominant normal gene was present in the purple locus than it was when the recessive purple was present. He also found that when the fly was of the constitution *Pr pr*, i.e., heterozygous for purple, the cross-over value for black-cinnabar was less than in flies of the constitution *Pr Pr*. This reduction in the cross-over value he attributes to the perceptible shortening of the chromosome by the dropping out of the gene dominant to purple

(see Fig. 27). When the fly is heterozygous for purple the two chromosomes will not be symmetrical, and this may interfere with

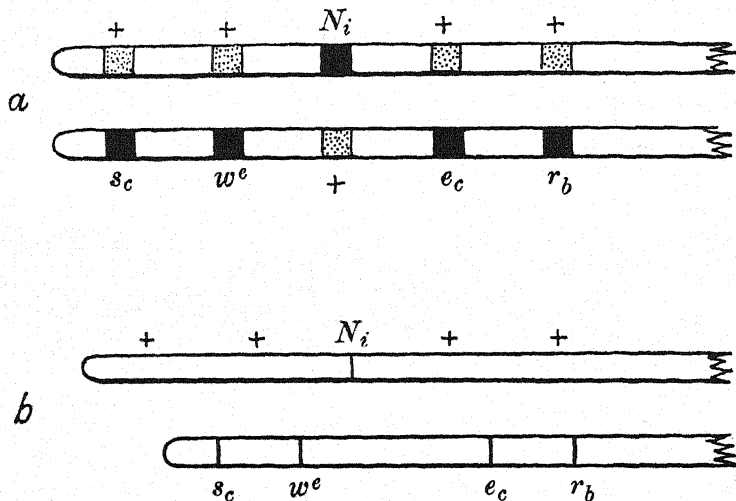


FIG. 27.—*a* represents some of the loci of factors in the sex chromosomes of *Drosophila melanogaster*. *b* represents the lengths of the sex chromosomes on the assumption that the recessives and N_i are absences. (Serebrovsky, Ivanova and Ferry, 1929.)

crossing-over. Serebrovsky thus returns to the presence and absence theory, but points out that, both it and Morgan's theory may require modification to the view that the gene is divisible.

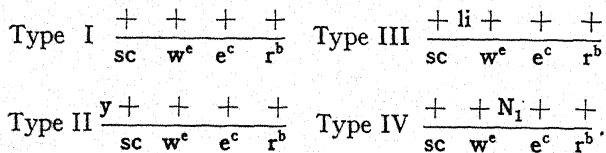


FIG. 28.

Later Serebrovsky, Ivanova and Ferry studied crossing-over at the left end of the sex chromosome of *D. melanogaster*. The regions were marked by scute sc , eosin w^e , echinus e^c , and ruby eye colour, r^b . The effect of introducing y , a recessive situated near scute, li , a recessive lethal between yellow and eosin and N_i , a homozygous

dominant lethal between eosin and echinus, upon the cross-over values between the above genes was examined.

The constitutions of the flies studied were therefore as in Fig. 28.

The authors show that the cross-over values in type I hybrid are lower than II, III or IV, and that type IV showed a marked increase in crossing-over in the region eosin echinus (where N_1 is situated. N_1 is probably an absence). Type III showed the greatest increase in the scute-eosin region, while type II showed a general increase.

TABLE 14

Summary of Cross-over Values in three experiments on the X Chromosome of Drosophila melanogaster involving Flies of four different constitutions. (see Fig. 28, Serebrovsky, Ivanova and Ferry, 1929)

		Regions			Total
		$Sc-W^e$	W^e-e_c	e_c-r_b	$Sc-r_b$
Type I	+	0.39 ± 0.05	2.18 ± 0.12	1.32 ± 0.09	3.89
„ II	y	0.61 ± 0.06	2.63 ± 0.13	1.67 ± 0.10	4.91
„ III	l_i	0.59 ± 0.06	2.49 ± 0.12	1.41 ± 0.09	4.49
„ IV	N_i	0.54 ± 0.06	2.83 ± 0.15	1.26 ± 0.10	4.63

		Regions			Total
		$Sc-W^e$	W^e-e_c	e_c-r_b	$Sc-r_b$
Type I	+	0.75	4.20	2.55	7.50
„ II	y	0.93	4.02	2.55	7.50
„ III	l_i	0.99	4.16	2.35	7.50
„ IV	N_i	0.88	4.58	2.04	7.50

		Regions			Total
		$Sc-W^e$	W^e-e_c	e_c-r_b	$Sc-r_b$
Type I	+	0.59	3.30	2.00	5.89
„ II	y	0.73	3.15	2.00	5.88
„ III	l_i	0.84	3.54	2.00	5.38
„ IV	N_i	0.86	4.49	2.00	7.35

		Regions		
		$Sc-W^e$	W^e-e_c	e_c-r_b
Non-	+	0.39	2.18	1.32
Ratio	+	0.58	2.65	1.44
		1.49	1.22	1.09

The authors attribute the increase to the resolution of asymmetry brought about by introducing recessive genes on the chromosome which carries most dominants. The influence of each recessive gene is most marked in the region of the chromosome to which each belongs, but the influence also extends with less effect to neighbouring regions. The authors assume, then, that the chromosome with the wild type allelomorphs of those they studied will be longer than that containing the recessive genes. Hence a certain asymmetry between the chromosomes results and interferes with crossing-over. When, however, a recessive gene such as *y* in type II is introduced into the chromosome carrying wild type allelomorphs, the asymmetry is reduced by the relative sizes of *y* and its dominant allelomorph.

While these experimental facts of Serebrovsky appear to be well substantiated, it is necessary to approach with caution the hypothesis put forward to explain them. Indeed, Sturtevant and Schultz (1931) bring forward evidence that Agol's results could be explained in a different way, more in keeping with the general view. They studied duplications of various portions of the *X* chromosome which included scute itself. Where the duplication includes a considerable portion of the *X* chromosome, as in a translocation to chromosome III of the *X* broken to the right of "white", it is found that scute behaves as a dominant, whereas with smaller portions of the duplicated *X* chromosome it behaves as a recessive. They point out therefore that the expression of scute varies with the balance of the gene to other factors, of which two at different loci on the *X* are known. Hence Agol's results may be explainable by the differential interactions of the different scute allelomorphs with other genes.

Thompson's Side-chain Hypothesis. The hypothesis of step allelomorphism implying a compound structure of the gene has some similarity with another—the "side-chain" hypothesis of Thompson (1931).

At the Bar locus of *Drosophila melanogaster* are a number of genes which control the number of facets or ommatidia of the compound eye. The size of the facet remains the same, but the number of facets varies with the particular allelomorph present. The number of facets of a normal fly is about 740, while Bar flies have 325. All

Bar flies originated from a single Bar-eyed male found by Tice in 1913 and no mutations of normal to Bar have been seen in millions of flies raised since then.

In 1917, however, May reported eleven occurrences of the reverse mutation from Bar eye to normal, round or full eye. Zeleny (1920) found another allelomorph ultra-Bar (double-Bar according to Sturtevant) which appeared in homozygous material of Bar flies. Round eye is incompletely recessive to Bar. Double-Bar also mutates to Bar and then to round eye, or it may mutate directly to round without passing through the Bar condition. The summary of the mutation rates is shown in the accompanying diagram (Fig. 29).

Sturtevant made a clever analysis of the relationships of Bar and double-Bar and also of another allelomorph, infra-Bar. He showed that any interchange of Bar and double-Bar or change to round eye was accompanied by crossing-over between "forked" and "fused,"

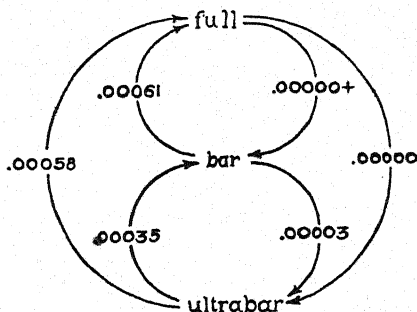


FIG. 29.—Mutation rates of normal, Bar and double-Bar genes. (Thompson, 1931.)

which are located to the right and left respectively of the Bar locus on the X chromosome. He therefore suggested that the change from Bar to double-Bar and the change to round eye was due to *unequal crossing-over* at the Bar locus. From an individual $\frac{fB}{Bfu}$, i.e.,

heterozygous for forked and fused and homozygous for Bar, unequal crossing-over could produce chromosomes of the constitutions fBB , fu , f , $BBfu$. Hence flies with the chromosome carrying fBB or $BBfu$ would have double-Bar eyes. If this is indeed the case then Bar should produce double-Bar and normal-eyed flies with equal frequencies.

The data of Sturtevant and of Zeleny (1919, 1920, 1921) show that normals are much more frequently produced than double-Bar from

Bar flies. Double-Bar is only 75% as viable as normal, so that fewer double-Bar flies are expected, but the latest figures (Sturtevant, 1928) obtained after critical examination of the flies, show that the ratio of normal to double-Bar flies is 1.9 normal to 1 double-Bar. However, as Sturtevant points out, the critical proof that unequal crossing-over of **B/B** flies gives double-Bar and normal, would be furnished by an instance of the two types arising as complementary products from one event of unequal crossing-over.

Morgan, L. V. (1931), who had been working with flies in which two *X* chromosomes were attached to one another at one end and each contained the factor **B**, provided this evidence. From this stock a narrow-eyed female appeared which resembled double-Bar flies. On Sturtevant's hypothesis crossing-over had taken place unequally near the Bar locus. Thus one of the chromosomes should have **BB** and the other should have no allelomorph if the hypothesis is correct. The female was mated to yellow normal-eyed males. If the female was the expected **BB/o** type, about 5% of her daughters would be normal, since forked exhibits 5.1% homozygosis (see p. 121) in attached *X* chromosomes through crossing over between that locus and the attachment constriction. If the female was of the constitution **BB/B** (not expected on the hypothesis) no normal-eyed daughter flies would be found. The mating produced 3 normal and 50 Bar-eyed females in the F_1 , and in the F_2 , 96 Bar-eyed and 6 normal-eyed females. The percentage of normal-eyed females is clearly too large to be accounted for by mutation reversion and is close to the 5% expected from unequal crossing-over.

Thompson (1931) also reports two cases of complementary products, double-Bar and normal, from Bar-eyed flies.

The most striking result is, therefore, that the difference between homozygous Bar and double-Bar is not a genic difference but a positional one. On separate chromosomes the Bar genes give the phenotype Bar, but when both of the genes are on the same chromosome and lying side by side the phenotype is double-Bar. (Muller (1930 *b*) reports a further case of positional effect in relation to mosaicism of the eyes of *D. melanogaster* after X-ray treatment.)

Another allelomorph of Bar called infra-Bar (**Bⁱ**) which gives

TABLE 15
(Goldschmidt, 1928)

Num- ber.	Homozygote.		Facet Number.	Num- ber.	Homozygote.		Facet Number.
	Formula.	Character.			Formula.	Character.	
1	$\frac{B}{B}$	normal	779.4	4	$\frac{B_1 B_1}{B_1 B_1}$	double- infrabar	38.2
2	$\frac{B_1}{B_1}$	infrabar	320.4	5	$\frac{B_1 B_2}{B_1 B_2}$	barinfrabar	26.7
3	$\frac{B_2}{B_2}$	bar	68.1	6	$\frac{B_2 B_2}{B_2 B_2}$	double- ultrabar	24.1

Num- ber.	Heterozygote.		Facet Number.	Num- ber.	Heterozygote.		Facet Number.
	Formula.	Character.			Formula.	Character.	
7	$\frac{B}{B_1}$	normal- infrabar	716.4	15	$\frac{B_1}{B_2 B_2}$	infrabar- ultrabar	41.8
8	$\frac{B}{B_2}$	normal-bar	358.4	16	$\frac{B_2}{B_1 B_1}$	bar-double- infrabar	38.3
9	$\frac{B}{B_1 B_1}$	normal-double- infrabar	200.2	17	$\frac{B_2}{B_1 B_2}$	bar- barinfrabar	37
10	$\frac{B}{B_1 B_2}$	normal- barinfrabar	50.5	18	$\frac{B_2}{B_2 B_2}$	bar-ultrabar	36.4
11	$\frac{B}{B_2 B_2}$	normal- ultrabar	45.4	19	$\frac{B_1 B_1}{B_1 B_2}$	double- infrabar- barinfrabar	27.9
12	$\frac{B_1}{B_2}$	infrabar-bar	73.5	20	$\frac{B_1 B_1}{B_2 B_2}$	double- infrabar- ultrabar	26.7
13	$\frac{B_1}{B_1 B_1}$	infrabar- double- infrabar	138.0	21	$\frac{B_1 B_2}{B_2 B_2}$	bar-infrabar- ultrabar	24.1
14	$\frac{B_1}{B_1 B_2}$	infrabar- barinfrabar	37.8				

292 facets, is a gene mutation at the Bar locus and behaves in a similar fashion to Bar. It reverts to normal and gives rise to double-infra-Bar. It can be seen at once that this affords a further

means of testing the hypothesis. Sturtevant pointed out that if unequal crossing-over took place in a fly of the constitution B/B^i , flies would be produced with B to the left or right of B^i . By linkage experiments, utilising forked and fused, he identified the two conditions postulated. Further, he found that individuals of the constitution BB^i/o thus produced did not revert to normal but to Bar or to infra-Bar. When these reversions took place, the reversion to Bar was accompanied by crossing over in the forked-Bar region, while reversions to infra-Bar were associated with crossing over in the Bar-fused region. This indicated that in the parent fly, Bar was situated nearer forked and infra-Bar nearer fused. In a different stock the reverse position was found.

Table 15 illustrates some of the possible combinations of B and B^i with "positional effect" on facet number.

Thompson (1931) has put forward an interesting theory which, if substantiated, combines the phenomena at the Bar locus with the phenomena at other loci into one general scheme regarding the nature of the gene.

His side-chain hypothesis is similar to that of Serebrovsky and Agol and their co-workers in that it supposes that the gene is divisible and that a linear distance may occur between the elements of the gene along the chromosome. Fig. 30 illustrates Thompson's hypothesis for the phenomena at the Bar locus.

The gene is supposed to be composed of a central body, the protosome, and it may have one or more subsidiary bodies, the episomes. The gene for normal eye consists only of the protosome and that for Bar eye of the protosome plus one episome which is attached to the protosome. The episome may have come from some other locus on the same or a different chromosome. Crossing over, irradiation, or non-disjunction, create circumstances in which the episome is disjoined from one protosome and becomes attached to another. Thus double-Bar would consist of the original Bar protosome and episome plus an episome derived from the homologous chromosome, due to conditions brought about by crossing-over (see Fig. 30).

If the episomes are joined one to another and one is attached to the protosome, the break down from the double-Bar condition to

Bar or to normal should be equal in frequency. The data of Zeleny and Thompson show that this is the case.

Infra-Bar is a true gene mutation, and Thompson suggests that its episome is different in kind from that of Bar; two different episomes will not be arranged end to end, but both will be attached to the protosome in an individual of the constitution BB^i/o . Hence a positional effect would be observed in linkage experiments.

The expression of the proportion of episomes to protosomes can apparently be described in the form of an exponential function. It had been found by Zeleny (1920) that the facet number of flies

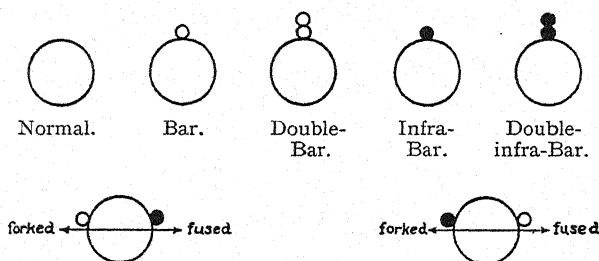


FIG. 30.—Diagrammatic explanation of the side-chain hypothesis. (Thompson, 1931.)

bearing different members of the Bar series had an exponential relationship. Thompson expresses the number of episomes in terms of facet numbers by

$$\log_{10} f(n) = a + bc^n$$

where n is the number of episomes and a , b and c constants determined by the different combinations of the four remaining facet types taken three at a time in an algebraic equation. Thus :

a is 1.263

b is 4.209

c is 0.276

The facet number, calculated from the number of episomes present, is close to the number observed, except in the case of normal eye which has been recognised by all workers as being qualitatively different and on the side-chain theory contains no episomes.

The following table illustrates the close correspondence between observed and calculated facet numbers :—

TABLE 16
(Thompson, 1931)

	Episomes Present in Females.	Calculated Facet Number.	Observed Facet Number.
Normal eye . . .	0	373.250	740
Bar (heterozygous) . . .	1	325	325
Double-Bar . . .	2	48.2	49
Bar, double-Bar . . .	3	28.3	28.1
Double-Bar, double-Bar . . .	4	24.4	24.5

This function theoretically approaches a limit at 23.1 with 7 episomes to 2 protosomes. Hence triple-Bar would be almost indistinguishable from homozygous double-Bar. In the infra-Bar series a similar calculation brings out the fact that no positive limit in facet number is approached, but that 6 episomes (3 on each protosome—homozygous triple-infra-Bar) would give almost no facets at all. Hence the practical limit is 3 episomes to 1 protosome in this case. The attempt by Sturtevant to synthesise triple-Bar and triple-infra-Bar failed.

It will be realised, therefore, that dominance, on this theory, is dependent on the threshold value of the ratio of protosomes to episomes, which varies with each particular case, but could be calculated when intermediate values are known. The formula for facet number in terms of episomes shows that there will be no change in facet number until the threshold value of 2 episomes to 1 protosome is reduced. Hence genes at the Bar locus with 4 or 5 episomes cannot be separated by their phenotypes, but allelomorphs with 3 or 4 may be separated by the fact that in heterozygotes with normal genes the ratio of episomes to protosomes in the first case is 4 : 2, giving complete dominance, and in the other case 3 : 2, an incomplete dominant. It should be noted, however, that the threshold value varies with the particular character being considered. The threshold value for ocellar bristles (the number of

which varies inversely to facet number and is controlled by the genes at the Bar locus) is above 0 episomes to 1 protosome, while the occurrence of median ocellus (which is usually absent in ultra-Bar) is below 2 episomes to 1 protosome.

Goldschmidt's Physiological Hypothesis. As a result of his work on *Lymantria dispar* and *L. japonica*, Goldschmidt (1922, 1923, 1927, 1931) put forward another theory of factor action which, if true, sheds considerable light on many genetical phenomena. He found that when European and Japanese races of the Gipsy moth were intercrossed, the sex ratio and degree of intersexuality depended on the particular races used, although when inbred each race had a normal sex ratio and behaviour.

The cross, European female \times Japanese male, gives normal males and females which are intersexual in the F_1 . The intersexual females when crossed with normal males give 50% normal females and 50% intersexual females. The reciprocal cross, Japanese female \times European male, gives normal males and females in the F_1 , but in the F_2 the males show intersexual tendencies. Different races from Europe and Japan have different degrees of strength of the male and female sex potencies. These were classified and predictions made of the result from any particular cross. If we designate the male potencies as M_1, M_2 , etc., and the female as F_1, F_2 , etc., where M_1 is a weak male determiner and M_5 a strong, the various crosses may be symbolised in a factorial manner.

The M factors behave as allelomorphs, while the F factor is either borne by the W chromosomes (moths have heterochromosomes and are WZ in the female and ZZ in the male) or in the cytoplasm.

A "weak" male $M_2M_2F_3$		\times		a "strong" female M_3mF_4	
gametes	M_2			M_3F_4 and mF_4	
F_1	$M_2M_3F_4$			M_2mF_4	
	male		\times	female	
	($M > F$)			($M < F$)	
gametes	M_2 and M_3			M_2F_4 and mF_4	
F_2	$M_2M_2F_4$	M_2mF_4	$M_3M_3F_4$	M_3mF_4	
intersexual male	female	male	female		
$M = F$	$M < F$	$M > F$	$M < F$		

Goldschmidt infers that the particular sex type depends on which sex potency is stronger during the time of development. The reaction chain of processes originating in the factors, which are supposed to be similar in their action to autocatalysts, are carried on at different but definite rates. The particular reaction process, which is uppermost at the end point of development has the greater influence upon the final character product.

This physiological hypothesis may be applied to almost any genetical result, but since attention has been previously directed to the Bar and scute cases we will only mention here Goldschmidt's (1927, 1931) interpretation of them. If we arrange the order as in Table 15, so that the effect of two similar genes in column 1, or a single gene in columns 2, 3 and 4 upon facet number can be seen, the facet number decreases with the change in allelomorph in a similar way in all columns except column 3. We know positively that the difference between rows number 4 and 2 is purely quantitative and depends on the number of infra-Bar genes present, and numbers 3 and 6 are also quantitative differences of the Bar gene. Goldschmidt holds that there is a quantitative difference between normal and the two allelomorphs, Bar and infra-Bar. Their effect on the facet number is similar in kind to the end products of several chemical processes which only differ in the speed of action. The quantity of factor present is proportional to the quantity of the end result with regard to any one allelomorph.

As regards the scute allelomorphs Goldschmidt (1931) points out that an interpretation on a physiological basis may be put forward. This supposes that each scute allelomorph sets in motion a train of reaction processes, which in rate of development is a function of the particular factor or factors present. If we have a series of reaction processes, the strength of each proportional to the initiating factor, we can arrange these in order of strength up to the point where the character expression is saturated. Thus a step-reaction instead of step allelomorphism summarises Goldschmidt's view.

Qualitative character differences can easily depend on quantitative amounts of factor. Thus some scute factors may only affect the bristles on the head and not those of the scutellum and dorsocentral region of the thorax. The differentiation of the head, scutellum and

dorsocentral region may be ended at different periods. Suppose that the different scute allelomorphs produce different rates of development of the reaction processes—then only those parts of the body which are being differentiated by the reaction processes of other factors at the same time will be affected by the scute allelomorph (*cf.* Fig. 31). Where there are two scute allelomorphs, the final character will be determined by the weighted mean of the two reaction processes.

Dominance of one factor over another is thus, according to

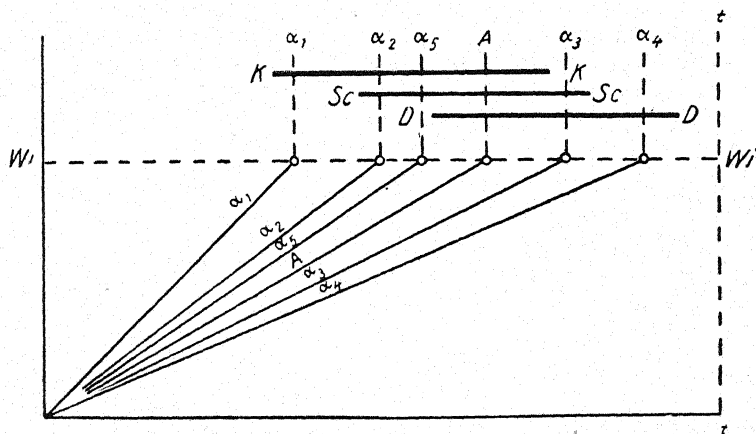


FIG. 31.—See text. (Goldschmidt, 1931.)

Goldschmidt, dependent upon the degree reached by the reaction process in the saturation of character expression at the end of the time of development.

The scute example shows that the extent of saturation depends not only on the reaction chain of one factor, but also on its relation to the reaction processes of other factors. In the above figure it will be seen that the head, scutellum and dorsocentral region are all affected by the dominant factor *A*, which has saturated the expression of bristles. As regards head bristles, *a*₁ may be considered dominant to *a*₈—the head and dorsocentral regions being differentiated at different rates. Therefore the slow rate of reaction of *a*₁ is able to

influence the development of the bristles on the head but not on the thorax. The thorax is supposed to develop quickly and would only be influenced by the factor reaction of the factor a_3 . Thus we see in Goldschmidt's theory an assumption of the factor being similar to an autocatalyst in action, and that dominance is a matter of saturation of character expression in any particular but defined genetical constitution.

Fisher's Theory of Dominance. A theory of dominance, the effect of which resembles the foregoing in some respects, has been put forward by Fisher (1928 *a, b*, 1930, 1931).

He pointed out that among 221 mutations in *Drosophila melanogaster* only thirteen were dominant to the wild type, while the remainder were recessive. Of the dominants, all showed incomplete dominance over the wild type. Where there is a series of multiple allelomorphs the wild type is completely dominant over the remainder, but the heterozygotes between any other two show incomplete dominance (see p. 139). If we are to assume that the wild type factor is generally completely dominant over the allelomorphs, as it appears to be, it is evident that the dominance must have been brought about by some particular cause. Fisher sees the cause to be natural selection.

It is known that when first found, a factor mutation is very distinct in type, but after several generations of inbreeding becomes less differentiated from the allelomorph in the wild type. The modification towards a wild type appearance is apparently due to selection of modifying factors which increase viability. Let us suppose that a mutation occurs with a frequency rate of one in a million in a wild population. It is obvious that the heterozygote will be much more frequent in the population than the mutant homozygote. If the heterozygote is 1% less viable than the wild type, the proportion of heterozygotes will be 1 in 5,000, and if it is 50% less viable the ratio of heterozygotes will fall to 1 in 750,000. The mutant homozygotes are proportional to the mutation rate, consequently the number of mutant homozygotes, in comparison with the number of heterozygotes, is negligible.

Selection, therefore, first acts upon the heterozygote. If it were at first intermediate between the wild type and the homozygous

mutant, any modification towards the greater viability of the wild type would be favoured by selection. Selection intensity increases rapidly as the viability increases, consequently any heterozygote, which was more similar to the wild type in viability would be more rapidly acted upon by selection and might become normal before those with an initially low viability had made any appreciable progress.

After the heterozygote is selected to the wild type characteristics, selection can start upon the recessive homozygote, which will now be much more frequent in the population. In favourable cases selection may be such that the recessive may become indistinguishable from the dominant.

Fisher supposes that selection of the modifying factors changes the character of the heterozygote from that of an intermediate type to that of the wild type.

Conclusion. The foregoing theories on the constitution of the factor or on the manner of factor action indicate that as yet we have comparatively little knowledge of the nature of the factor itself. The presence and absence theory, the step allelomorph theory and side-chain theory agree in attributing in some way a quantitative difference between the dominant and recessive allelomorphs. Goldschmidt's physiological theory and Bridge's theory of genic balance (see p. 250) agree in showing that there is a quantitative effect of factor action. In many cases a difference in this quantitative effect between two allelomorphs may be observed; nevertheless, in all the theories a qualitative difference is implied between non-allelomorphic factors and in some cases between allelomorphs.

The general conclusion from the experiments and theories on the constitution of the factor can be summarised as follows. The nature of the factor itself is at present unknown. One allelomorph differs from another, either qualitatively or perhaps more frequently quantitatively. The relative expression of two allelomorphs probably depends on the relative rates of factor action in a determined genetical background.

CHAPTER IV

THE ORIGIN OF POLYPLOIDY

Introduction—Somatic Doubling—Doubling in Gametogenesis

Introduction. Each type of chromosome present in the basic or haploid complement of an organism is represented twice in the diploid form. If the haploid set be represented by n then the diploid number of chromosomes will be $2n$, the triploid $3n$, tetraploid $4n$, and so on. The realisation that polyploid forms are extremely common in nature, has considerably changed the viewpoint of geneticists. The first reported case of tetraploidy under controlled conditions was that of the *gigas* mutant of *Oenothera Lamarckiana* which appeared in the cultures of de Vries. This plant was shown by Gates (1909) to have larger cells and larger nuclei containing 28 chromosomes in place of the usual 14 of the diploid (Lutz, 1907). Since then numerous polyploids have arisen in experimental material. Among the best known are:—*Primula Kewensis* (Newton and Pellew, 1929), *Raphanus-Brassica* (Karpechenko, 1924, 1927 a, b, 1928), *Solanum nigrum*, *Solanum Lycopersicum* (Winkler, 1916, Jørgensen and Crane, 1927, and Jørgensen, 1928), *Primula sinensis* (Gregory, 1914, Gregory, de Winton and Bateson, 1923), *Nicotiana sp.* (Clausen and Goodspeed, 1925, Rybin, 1927, and Brieger, 1928 a), *Crepis* (Navashin, 1925 b), *Saxifraga pottermensis* (Marsden-Jones and Turrill, 1930), *Phleum* (Gregor and Sansome, 1930), *Musci* (Marchals, 1907, and Wettstein, 1924 a), *Datura Stramonium* (Blakeslee, Belling and Farnham, 1923).

In a diploid, the chromosome number of the gametophyte is haploid and generally corresponds with the basic number, except in certain cases generally known as diploids, which later will be shown to be complex polyploids or "secondary polyploids" and not true diploids in the accepted sense of the word (see p. 234). In polyploids, however, the so-called haploid number of the gametophyte does not

correspond to the basic number. For convenience $2n$ is used to represent the somatic number and n the haploid or gametic number of a particular plant, while x represents the basic number of the group to which the plant belongs.

The lists of Tischler (1927, 1931) and Gaiser (1926, 1930 *a, b*) give the chromosome numbers of several thousand flowering plants. These plants belong to about five hundred genera of diverse natural orders. About one-sixth of the genera included, consist of species which have straight polyploid numbers, *i.e.*, they are multiples of a common basic number x . For example, the species of *Chrysanthemum* have somatic numbers 18, 36, 54*, 72*, 90*, *i.e.*, $x = 9$ (Tahara, 1921). *Solanum* species have somatic numbers 24, 36, 48, 60, 72, 96, *c.a.* 108, 120, *c.a.* 144 therefore $x = 12$ (Jørgensen, 1928, Jørgensen and Crane, 1927, Vilmorin and Simonet, 1927 *a, b*, 1928). In the first case the species with the highest chromosome number has ten sets of the basic number of the genus (decaploid). Other genera such as *Solanum* may have species with an even higher multiple number.

In a few cases the species of a genus may be divided into two distinct polyploid series. *Papaver* has species with chromosome numbers 14, 28, 42, 70, and 22, 44 (Ljungdahl, 1922, 1924), and the two basic numbers are $x = 7$ and $x = 11$. We shall see later that this diversity in the basic number is significant in defining inter-relationships. Winkler introduced the word *heteroploid* to include both the straight polyploids and those plants which have irregular numbers such as $2x + 1$, $3x - 1$, etc. Täckholm (1922) further divided heteroploid numbers into *euploid*, *i.e.*, straight polyploid and *aneuploid*, *i.e.*, irregular numbers.

It has been found that polyploids may originate in either of two ways.

- (1) By doubling of the chromosome number in the somatic tissue.
- (2) By formation of gametes containing either the unreduced number of chromosomes or at least containing more than the haploid complement of chromosomes.

The genetical consequences of these two methods of doubling of the chromosome number may be different for the following reasons.

* The haploid numbers were counted.

Where the doubling takes place in the somatic tissue, the resultant polyploid form naturally contains a double complement of the chromosomes and factors present in the original form. Hence there is no qualitative difference, but a quantitative difference in factor content between the diploid and its derivative tetraploid forms. On the other hand, formation of gametes with more than the haploid complement of chromosomes may or may not give a similar result to that of somatic doubling. If a gamete is formed by a division, in which the reduction phase, characteristic of meiosis, is nullified, and if this gamete is fertilised by one similarly formed in the same plant, then the resulting polyploid will have a chromosome constitution identical with that of a polyploid formed by somatic doubling. If, on the other hand, polyploid gametes are formed in any other way the chromosome complement resulting from their union will be different from the complements arising from somatic doubling.

Somatic Doubling. Direct evidence as to the method of origin of particular polyploids is generally difficult to obtain.

The origin of the tetraploid *Primula Kewensis* is a good example of the doubling of the chromosome number in the somatic tissue. It was first reported by Digby (1912) and later by Newton and Pellaw (1929). The sterile diploid hybrid between *P. floribunda* ($2n = 18$) \times *P. verticillata* ($2n = 18$) produced one branch with fertile flowers. Tetraploid offspring ($2n = 36$) which bred approximately true were obtained from this branch, which had double the chromosome number of the rest of the plant tissue.

The fertile tetraploid hybrid *Saxifraga potternensis* probably arose in a similar way from the sterile diploid hybrid of *S. rosacea* ($2n = 32$) \times *S. granulata* ($2n = 32$) (Marsden-Jones and Turrill, 1930). Whyte (1930) states that the hybrid probably arose by doubling of the chromosomes as a result of abnormal meiosis in the hybrid F_1 . Sansome (1931), however, pointed out that by this method seed production would be small and that the seeds would be formed irregularly over the diploid F_1 plant. Somatic doubling in a sterile hybrid, on the other hand, gives rise to greater fertility in that part which has doubled. The seed production of the *Saxifraga* hybrid F_1 is reasonably high, and is approximately equal to that of the derived tetraploid generation. Sansome therefore concluded

that *S. potternensis* arose from an F_1 plant which had the tetraploid number of chromosomes in at least a part of its tissue, i.e., somatic doubling. Whyte (1932), however, after further observations retains his original views.*

Another example of somatic doubling in branches was found by Blakeslee and Belling (1924 a, b). On several occasions, chiefly after cold treatment, tetraploid branches with 48 chromosomes were found on normal diploid plants ($2n = 24$) of *Datura Stramonium*. These branches were fertile and gave tetraploid progeny. Branches of abnormal appearance were also observed on normal diploid plants, and were found to be aneuploid in chromosome constitution. In two cases a chromosome had been lost from the complement, i.e., instead of the branch having 24 chromosomes it had 23, or in symbols $2x - 1$. In one case an extra chromosome was present, i.e., $2x + 1$.

Nicotiana glutinosa ($2n = 24$) \times *N. Tabacum* var. *purpurea* ($2n = 48$) normally gives sterile triploid hybrids. Clausen and Goodspeed (1925), however, found one F_1 plant which set seed when selfed artificially, but not when naturally pollinated. The selfed progeny were found to be hexaploids ($2n = 72$), and were also reasonably self-fertile and cross fertile with the parent species. These workers believed that this particular F_1 plant had doubled its number of chromosomes soon after fertilisation and therefore had become a hexaploid. This hexaploid is known as *N. digluta*.

A tetraploid seedling tomato was found by Lesley and Lesley (1930) in the progeny of a cross between a double trisomic plant with 26 chromosomes ($2x + 1 + 1$) and a diploid with 24 chromosomes. They state that if the tetraploid arises by fusion of two diploid gametes the formation of these diploid gametes is difficult to explain. If non-reduction took place in meiosis the two extra chromosomes of the double trisomic female parent would still be present and the number of chromosomes in the progeny would be 50 and not 48. If reduction was preceded by doubling, the constitution before meiosis would be $4x + 4$. In all probability the 4

* Since going to press it has been found (Philp, unpublished) that the *rosacea* parent was a tetraploid and the hybrid F_1 was a triploid. The production of polyploid gametes by the F_1 , and hence the origin of the tetraploid *S. potternensis*, is thus accounted for. These observations should be remembered when *S. potternensis* is quoted in other parts of the text.

chromosomes in excess would associate in pairs or would associate with the groups of 4 with which they were homologous to form sexavalents. Such behaviour would not lead to loss of all the extra chromosomes. On the other hand, trisomic plants give more diploid plants than one would expect in their progenies since the extra chromosomes are eliminated during gametogenesis. Therefore by elimination of the extra chromosomes the double trisomic might form haploid gametes. Lesley and Lesley, therefore, suggest that this tetraploid arose by somatic doubling after fertilisation in a similar manner to that suggested by Clausen and Goodspeed for their hybrid *Nicotiana* and by Blakeslee, Belling and Farnham (1923) for their tetraploid *Daturas*. Incidentally, this tetraploid showed no signs of injury or callus formation, which was known from Jørgensen and Crane's work to be associated with doubling of the chromosome number.

These are a few examples where a polyploid form has arisen naturally under experimental conditions as a result of the doubling of the chromosome number in the somatic tissue. Increase in the chromosome number of somatic cells has been observed in plants. Generally, however, the occurrence in diploid plants, of somatic cells which are tetraploid, hexaploid or aneuploid is comparatively rare.

Polyploid somatic cells have been observed by Huskins and Smith (1932) in *Sorghum* (4x), Philp (unpublished) in *Primula sinensis* (4x), Crane and Darlington (1927) in a triploid *Rubus* hybrid (6x), Mann Lesley (1925) and Winkler (1916) in *Solanum Lycopersicum* (4x) and (4x + 4), Philp (unpublished) in *Narcissus* (2x + 1), Darlington (1926) in *Scilla* (2x + 1 and 2x - 1), Stomps (1910), and de Litardière (1923) in *Spinacia* (4x), de Litardière (1924) and Breslawetz (1926) in *Cannabis sativa* (4x), Strasburger (1907) in *Pisum sativum* (2x + 1), Winge (1917) in *Tragopogon pratensis*, and Terby (1924) in *Butomus umbellatus*, Navashin (1926) in *Crepis tectorum* and *C. dioscoridis*, and Webber (1930 a) in *Nicotiana sylvestris* (4x).

Although the occurrence of tetraploid somatic cells is not common, binucleate somatic cells are frequent, particularly near the growing point and in the pith and tapetum. Prankerd (1915) and Beer and Arber (1919, 1920) demonstrated the presence of binucleate cells in all of the 177 species from 60 families that they examined. Arber stated that the binucleate condition was invariably connected

with mitosis and did not result from amitosis or direct nuclear division. It seems possible that tetraploid cells might arise through the fusion of the nuclei in a binucleate cell. Jørgensen (1928) indeed is of the opinion that tetraploid cells in *Solanum* take their origin from the formation of binucleate cells by a nuclear division without the concomitant cell wall formation. This process he calls "endoduplication."

adiv Polyploidy in somatic cells of plants, especially in growing root tips, has been artificially induced by rise of temperature, wounding and by the action of chemicals such as chloral hydrate, and quinine sulphate (Nemec, 1904, 1910, and others). Further, Wettstein, El. and Em. Marchal and others have artificially induced doubling of the chromosomes in various mosses. By cutting the sporophyte and culturing on agar they obtained a protonema (gametophytic generation) which developed directly from the seta or sporogonium. The elimination of the reduction division, therefore, produces a gametophyte with the diploid number of chromosomes. The sex organs on this gametophyte are functional and fertilisation produces a sporophyte with the tetraploid number of chromosomes. This process can be repeated, giving rise to an octoploid sporophyte.

Polyploid forms of *Solanum* have been obtained as adventitious shoots. Winkler (1916), during his experiments with chimæras of *S. Lycopersicum* and *S. nigrum*, found in two cases that the tissue of *S. Lycopersicum* had 48 chromosomes instead of 24 chromosomes, while in one case *S. nigrum* had 144 instead of 72. The doubling of the chromosome number had produced a tetraploid *S. Lycopersicum* and what is virtually a duodecaploid *S. nigrum*. The process of formation of the chimæras of *S. nigrum* and *S. Lycopersicum* consists in grafting the two species together and cutting across the union. A callus is formed and from beneath it adventitious shoots arise. Some of these shoots prove to be chimæras. Jørgensen and Crane (1927), Jørgensen (1928), and Sansome (1930) developed the method and showed that the callus formation and not the grafting was the essential condition for the induction of somatic doubling of the chromosomes. The procedure was to decapitate young plants in vigorous growth and to suppress completely the formation of the axillary shoots. Adventitious shoots were developed by the procambium beneath the callus and about 6% of these shoots had

double the number of chromosomes of the original stock. It is possible that the artificial induction of somatic doubling of chromosome number may in the future be extended to other genera and prove a useful method of polyploid synthesis. We understand that at least two other genera, one in the Cruciferae and one in the Salicaceae can be dealt with in this manner.

Doubling in Gametogenesis. It is, however, more common to obtain polyploids by irregularities of meiosis in the parents than from somatic doubling of chromosomes. Cytological evidence as to the methods of origin of polyploid gametes is abundant. There are several ways in which polyploid gametes may be formed. In all cases they are the results of abnormalities in gametogenesis and for convenience may be grouped under four heads (*cf.* Darlington, 1930 *a*) :—

- (A) The first or second meiotic division is nullified.
- (B) The chromosomes divide equationally twice.
- (C) Syndiploidy or the formation of binuclear germ mother-cells.
- (D) The first division is completely suppressed.

It is not within the province of this book to deal with all the known cases where the above types of abnormalities have been observed, but Darlington has made a list of these cases under the above heads. To it must be added his own findings in *Prunus*, which come under the first three classes.

Darlington's list contains the abnormalities which have been observed cytologically, and all types of abnormality mentioned have not necessarily given rise to polyploid plants. He also includes haploid plants which produce gametes containing the same number of chromosomes as the somatic cells (*i.e.*, unreduced gametes), but these gametes are haploid and upon fertilisation will give rise to diploids and not to polyploids.

The first type of abnormality—nullification of the first or second division—arises generally through the lagging of the chromosomes at the division so that they form a bridge between the two main groups of chromosomes at anaphase. The formation of two distinct nuclei is thus prevented. At the first division this lagging of the chromosomes may be a result of failure of pairing of the chromosomes. At the second division this lagging sometimes results from

the fact that the chromosomes may have undergone an equational in place of a reductional division at the first nuclear division. A "restitution nucleus," first described by Rosenberg (1917) and again (1927), formed as the result of failure of the first division (or semiheterotypic division) does not always give rise to diploid dyads, but, as Meurman (1929) has shown in *Aucuba*, may result in the formation of multinucleate cells. Failure at the second division, however, usually gives rise to a triad of one diploid and two normal haploid nuclei, while other irregular arrangements may also result.

Failure of pairing of the chromosomes is usually due to a lack of homology. It is to be expected in species hybrids, but has also been reported by Rybin (1927) in *Nicotiana Tabacum*, which is not regarded as a species hybrid by systematists, although Goodspeed and Clausen (1928) on cytogenetic grounds consider that it is probably of hybrid origin. Therefore the homology of chromosomes in a plant cannot be ascertained by a knowledge of the taxonomic status of the plant alone. Abnormalities in gametogenesis have also been induced by artificial means such as low temperature and the action of chemicals. The literature up to 1916 on the influence of chemicals and cold treatment upon gametogenesis has been reviewed by Winkler (1916). Later experiments and observations have been carried out by Sakamura (1920), Borgenstam (1922), de Mol (1923 a, b), Michaelis (1926), Sakamura and Stow (1926), Stow (1926) and Shimotomai (1927). De Mol was successful in inducing the formation of giant diploid pollen grains in hyacinths by artificial means, and found them to be viable, since triploid progeny were obtained by pollinating diploid plants with them. These cytological abnormalities are sometimes localised upon the plant in *Prunus* (Darlington, 1930 a) and in the hybrid *Digitalis* (Buxton and Newton, 1928). The production of fertile seed is also confined to definite parts of the plant. This localisation is regarded by these authors as being due to the effect of external influences. Rybin (1927) considers that the formation of restitution nuclei in *Nicotiana* is due to a fall in temperature.

The second type of abnormality (the chromosomes divide equationally twice) is much less common than the first and is associated with complete failure of pairing of the chromosomes.

Induced

This class of abnormality has therefore been found almost exclusively in species hybrids. A tetrad of diploid spores is formed as a result of the chromosomes dividing equationally at the first and second meiotic divisions.

The third type of irregularity, "syndiploidy," does not appear to be directly connected with failure of pairing, or with hybridity, since it occurs, both in hybrids such as *Raphanus-Brassica*, and in non-hybrid material (Maize, Beadle, 1931).

Darlington regards syndiploidy rather as the first stage of contabescence in an anther, related perhaps therefore to male sterility, which occurs in *Prunus persica* and *Prunus domestica* (Crane and Lawrence, 1929), and which is a genetic factor in *Rubus* and elsewhere (Crane, 1926).

The consequence of syndiploidy is that diploid gametes are produced, or, when in addition, the first division is nullified, dyads of spores are formed each with the tetraploid number of chromosomes.

The fourth type of abnormality is cytologically distinct from the first type in that the first division is completely suppressed, and not the result of a first division being nullified.

Polyploid gametes, or rather aneuploid gametes, may be formed as a result of further irregularities in the above four main types of abnormal behaviour. For example, in the first type all the chromosomes may not be included in the "restitution nucleus." Each chromosome and its homologue has the potentiality of anomalous behaviour, independently of the remaining chromosomes. Hence, opportunity is given for the production of gametes with more or less than the normal reduced chromosome number.

The genetical consequences resulting from the four types of abnormality are different.

In syndiploidy pairing and disjunction of all or any of the homologous chromosomes can take place, and therefore the resulting nuclei may be different in factor content, from one another and from the original parent. In the remaining three types no heterotype division takes place, or if it does the result of the division is nullified by the inclusion of all the separated chromosomes within one nucleus. Therefore in these three types of abnormality, there is no

qualitative change of the chromosome complement from that of the somatic complement of the parent. There may, however, be a quantitative change such as the formation of a tetraploid gamete when the somatic tissue is diploid.

Naturally inference plays a large part in deciding the mode of origin of polyploid gametes. The cytology of the parent will sometimes throw light on this question, but often the decision depends on the behaviour of the succeeding derivative polyploid plants themselves. For this reason there are only a few cases in which the evidence is adequate to decide the exact mode of origin of a special polyploid gamete.

The following are examples of polyploids which have arisen in experimental interspecific hybrid material from hybrid F_1 plants (the hybrid *Raphanus-Brassica* is, of course, intergeneric). We shall divide them into two classes: (a) those polyploids which have arisen through the fusion of two unreduced gametes and are fertile, (b) those which have resulted from the fusion of an unreduced egg with a normal pollen grain. In interspecific hybrids of *Digitalis*, *Raphanus-Brassica*, *Phleum*, *Nicotiana* and *Fragaria* we have examples of the first class.

Digitalis purpurea ($2n = 56$) \times *D. ambigua* ($2n = 56$) gave practically sterile F_1 hybrids ($2n = 56$) and their selfed progeny had double the chromosome number ($2n = 112$) (Buxton and Newton, 1928).

On crossing *Raphanus sativus* ($2n = 18$) with *Brassica oleracea* ($2n = 18$) Karpechenko (1924, 1927 a, b, 1928), obtained hybrids with 18 somatic chromosomes. Most of these hybrids were self-sterile, but a few were slightly fertile and gave an F_2 progeny consisting mainly of tetraploids ($2n = 36$), a few hypertetraploids ($2n = 37-38$) and a few with approximately the hexaploid number ($2n = 54$).

Phleum pratense ($2n = 14$) \times *Phleum alpinum* ($2n = 28$) gave almost sterile triploid hybrids ($2n = 21$), but Gregor and Sansome (1930) succeeded in raising a progeny of four plants which were hexaploid ($2n = 42$).

Lammerts (1931) found that most of the F_2 progeny from the triploid hybrid *Nicotiana rustica* ($2n = 48$) \times *N. paniculata*

($2n = 24$) were approximately hexaploid with about 72 chromosomes.

By selfing the F_1 hybrid of the cross *Fragaria bracteata* ($2n = 14$) \times *F. Helleri* ($2n = 14$) Ichijima (1926, 1930) obtained a tetraploid plant ($2n = 28$).

In all these cases, with the exception of *Nicotiana*, the respective authors have obtained cytological evidence indicating that the F_1 produces unreduced gametes. It is noteworthy that except for *Fragaria* the F_1 hybrids were more or less sterile. This is largely due to abnormal meioses, leading to the production of unbalanced gametes (see p. 241). Doubling of the chromosome number of these sterile hybrids has led to normal meiosis and hence to normal fertility. Further, the tetraploids of *Digitalis* and *Raphanus-Brassica* were almost identical morphologically with the diploid hybrids. The tetraploid *Fragaria* breeds approximately true and is probably of the same nature as *Primula Kewensis* in being an allotetraploid with predominant autosyndesis (see p. 178).

In the second class we have *Galeopsis pubescens* ($2n = 16$) \times *G. speciosa* ($2n = 16$) which gave highly sterile F_1 plants ($2n = 16$). Six F_2 plants consisted of five diploids and one triploid ($2n = 24$) (Müntzing, 1930a). F_1 hybrids of *Salix viminalis* ($2n = 38$) \times *S. caprea* ($2n = 38$) were found by Håkansson (1929 a) to have 38 somatic chromosomes. The F_2 plants were diploids with the exception of two which were heteroploids. One was a triploid ($2n=57$) and the other was the sterile hypertetraploid ($2n=82-84$) known as *S. Laurina*. This example is almost identical with that of *Galeopsis*.

Brieger (1928a) crossed the tetraploid *Nicotiana Tabacum* ($2n=48$) with the diploid *N. Rusbyi* ($2n = 24$) and obtained triploid hybrids with 36 chromosomes. The hybrids back-crossed with *N. Tabacum* gave among their progeny one pentaploid ($2n = 60$) and one plant containing approximately 55 chromosomes.

In all these F_1 hybrids irregularities were observed at meiosis, e.g., fusion of the homotypic spindles, giving rise to unreduced gametes so that without doubt these polyploids arose through fertilisation of an unreduced egg with a normal pollen grain. It is probable that 24 of the 55 chromosomes of the *Nicotiana* plant are

derived from the male parent *N. Tabacum*, while the remaining 31 are derived from the triploid hybrid.

The following group of polyploids are those which have arisen directly from a cross and they all belong to the class in which an unreduced egg has been fertilised by a normal pollen grain.

Nicotiana Tabacum ($2n = 48$) when crossed with the diploid *N. sylvestris* ($2n = 24$) gave 50 F_1 plants of which 49 were sterile triploids ($2n = 36$) and one was a fertile pentaploid ($2n = 60$) (Webber, 1930 b). *Nicotiana Tabacum* var. *Dubek* ($2n = 48$) \times *N. rustica* (Turkestan var. *Kolmak*) ($2n = 48$) gave two self-sterile hybrids (Eghis, 1927). One of these hybrids TR_1 was found by Rybin (1927) to be a hexaploid ($2n = 72$). TR_1 was fertile when crossed with other varieties of *N. Tabacum* or with varieties of *N. rustica*. $TR_1 \times N. rustica$ var. *texana* gave five plants, of which one 0156/256 proved to be an octoploid with 96 chromosomes. 0156/256 was self-fertile and like TR_1 was cross fertile with other varieties of *N. Tabacum* and *N. rustica*.

The pollination which gave rise to TR_1 was carried out during cold weather in autumn and that giving rise to 0156/256 just after an abrupt fall in temperature. Low temperature has led to the production of unreduced gametes in *Nicotiana Tabacum* var. *Dubek* and in other species, and it is therefore concluded that this is the explanation of the origin of these polyploid *Nicotiana* plants. From the following evidence it is believed that the extra chromosomes of TR_1 and 0156/256 are derived from the respective female parents. TR_1 shows greater similarity to *N. Tabacum* than the tetraploid hybrids of the reciprocal cross (i.e., $TR_1 = 48T + 24R$).

The sister plants of 0156/256 were intermediate between *N. Tabacum* and *N. rustica*, while 0156/256 resembled *N. rustica* more so than TR_1 (i.e., $0156/256 = 48T + 48R$).

Similar results to those obtained by Eghis and Rybin with their *Nicotiana* hybrids have been found in *Galeopsis*. The triploid hybrid *Galeopsis pubescens-speciosa* ($2n = 24$) previously mentioned, when back-crossed with *G. pubescens* ($2n = 16$) produced a single fertile tetraploid plant ($2n = 32$) (Müntzing, 1930 b).

Fusion of the homotypic spindles was observed in meiosis of the triploid, thus providing evidence for the production of unreduced

gametes. The tetraploid, like the triploid, was morphologically undistinguishable from *G. Tetrahit*. Meiosis was normal and in genetical behaviour like *G. Tetrahit*. It was self-fertile and crossed readily with *G. Tetrahit*, but reciprocal crosses with its ultimate ancestors *G. pubescens* and *G. speciosa* gave no seed. The tetraploid derivative is therefore similar to the Linnean species *G. Tetrahit*, but it has been produced experimentally.

Rubus rusticanus inermis ($2n = 14$) \times *R. thyrsiger* ($2n = 28$) gave three hybrid plants referred to as RT_2 , RT_3 and RT_4 . The first two were sterile triploids ($2n = 21$) while RT_4 was a fertile tetraploid ($2n = 28$) (Crane and Darlington, 1927).

Diploid gamete formation has not been observed in *R. rusticanus*, but it has been seen in a related *Rubus* species. It is believed that the tetraploid RT_4 probably arose by fusion of an unreduced egg of the female diploid parent *R. rusticanus* with a normal diploid pollen-grain of the tetraploid male parent *R. thyrsiger* for the following reasons. The triploid sister plants of RT_4 approached the tetraploid parent in type while RT_4 exhibited four characters which were only shown by the diploid parent (i.e., $RT_4 = 14R + 14T$).

The following polyploids have arisen spontaneously within a diploid species. The first class has presumably arisen from the union of two unreduced gametes. Blakeslee, Belling and Farnham (1923) first discovered a tetraploid *Datura Stramonium* ($2n = 48$) in 1916 among the progeny of the diploid species ($2n = 24$). In 1919 five and possibly six more tetraploids were discovered. Tetraploid forms of *Primula sinensis* ($2n = 48$) were found among a batch of diploid plants by Gregory (1914) and Sömme (1930).

The second class have probably resulted from the fusion of an unreduced egg with a normal pollen grain giving triploids. Among their cultures of *Zea Mays* ($2n=20$) Randolph and McClintock (1926) found one triploid plant ($2n = 30$). Similarly Lesley and Lesley (1930) found three triploids ($2n = 36$) amongst about 9,000 normal diploid tomato plants ($2n = 24$). Triploids appear to arise more frequently in progeny of plants with an unbalanced chromosome number since six triploids were found among 2,000 plants in the progeny of trisomic plants (see p. 242).

In the progeny of a plant of *Crepis capillaris* ($2n = 8$) Navashin (1925 b) found one triploid ($2n = 12$) and one pentaploid ($2n = 20$).

It is difficult to obtain cytological evidence for the production of unreduced gametes in normal diploids since meiosis is generally regular. Further the rare occurrence of polyploids indicates how seldom an abnormality occurs in meiosis. In maize cultures, however, a few cases of binuclear microsporocytes containing 20 bivalents at first metaphase have been observed. Low temperature is known to cause the production of unreduced gametes and this may be the reason for the production of a diploid and tetraploid gamete by the *Crepis* plant which had been grown under abnormal climatic conditions. In *Datura* the fact that most of the tetraploids appeared in one season also makes one suspect a similar environmental cause for the formation of diploid gametes. Moreover, the genetical constitution of the diploid parents and of the tetraploids showed that the reduction division had taken place before the origin of tetraploidy. The possibility of apogamy of a $4x$ egg cell as suggested by Gates (1915) for the origin of tetraploids in *Oenothera* is therefore eliminated and likewise the possibility of apomixis. It appears likely that doubling of the chromosome number in *Datura* happened soon after the reduction division, but there is also the possibility that it took place very early in the zygote.

Darlington (1931 c) has summarised the pertinent facts regarding the origin of tetraploids in *Primula sinensis*. He points out that the absence of spontaneous triploids as in *Datura*, suggests somatic doubling to be the origin of some tetraploids.

CHAPTER V

AUTOTETRAPLOIDS

Introduction—Cytology—General Characteristics—Inheritance—Quantitative Expression.

Introduction. In a polyploid with more than two sets of chromosomes the possibilities at meiosis are more complex than in diploids. If the polyploid is composed of reduplicated sets of the normal diploid complement as in the somatically doubled tetraploid tomato, where the four sets are all homologous, pairing and the consequent disjunction may take place between parts of any two of four homologous chromosomes. This autopolyploid, adopting Kihara and Ono's terminology, differs from an "allopolyploid" where dissimilar sets of chromosomes are included in one plant. The tetraploid *Primula Kewensis* contains two sets of *P. verticillata* and two sets of *P. floribunda* chromosomes, and is therefore an allopolyploid. In autopolyploids only autosyndesis (*i.e.*, pairing of chromosomes of similar sets or descent) can take place, but in allopolyploids both auto- and allosyndesis can occur. For example, in the hybrid between *Papaver striatocarpum* ($2n = 70$) and *P. nudicaule* ($2n = 14$) Ljungdahl (1924) found that 21 bivalents were formed. This is assumed to result from internal pairing among the *striatocarpum* complement (autosyndesis) and pairing of the complement of *nudicaule* with 7 of the *striatocarpum* chromosomes (allosyndesis).

In the allotetraploid *Primula Kewensis* the *verticillata* chromosomes generally pair among themselves and the *floribunda* chromosomes do likewise (autosyndesis), but Newton and Pellew (1929) found that occasionally four chromosomes were associated, indicating that two of the *verticillata* and two of the *floribunda* chromosomes had together formed a quadrivalent (allosyndesis). Only autosyndesis occurs in the allopolyploid *Nicotiana digluta* (Clausen and Goodspeed, 1925), which contains two sets of *N. Tabacum* chromo-

somes and two sets of *N. glutinosa* chromosomes; 24 *Tabacum* bivalents and 12 *glutinosa* bivalents are formed.

These types of pairing—auto- and allosyndesis have a definite effect on the segregation of characters. The genetics of autopolyploids in which only autosyndesis occurs will be dealt with first.

Cytology. The cytology of autotetraploids on which genetical work has been done, is known for *Primula sinensis* (Sömme, 1930, Darlington, 1931 c), *Datura Stramonium* (Belling and Blakeslee, 1923, 1924 a; Blakeslee, Belling and Farnham, 1923) and *Solanum Lycopersicum* (Jørgensen, 1928; Lesley and Lesley, 1930). Lawrence (1929, 1931 a) has described the behaviour of the chromosomes in the allo-octoploid *Dahlia variabilis*, which shows tetrasomic inheritance for some characters.

The formation of quadrivalents as well as bivalents at heterotypic metaphase may lead to the occasional production of gametes with more or less than the $2x$ number of chromosomes. Further, instead of one chromosome pairing with another and then disjoining to the opposite pole as in a bivalent (normal disjunction) the formation of a multiple association of four chromosomes will sometimes lead to chromosomes or parts of chromosomes which have paired at prophase going to the same pole at anaphase (non-disjunction) (see p. 83). Non-disjunction in a quadrivalent can give rise to two abnormalities in the formation of gametes, both of which affect the heritable constitution of the gametes. Either there may be an unequal numerical distribution of the chromosomes to the gametes i.e., numerical non-disjunction, (*vide* Darlington, 1931 c), or genetical non-disjunction where the gametes have the $2x$ number of chromosomes, but some parts of the chromosomes which had paired appear in the same gamete instead of in different gametes (see Fig. 32).

All the chromosomes of *Datura* may form quadrivalents. but the average for *Primula sinensis* is 10.4 quadrivalents and 3.2 bivalents (Darlington, 1931 c). Jørgensen (1928) found only one or two quadrivalents in his somatically doubled tomato, but the Lesleys (1930) found 7–12% quadrivalents in a tetraploid tomato raised from seed. Darlington has suggested that the differences in quadrivalent formation between the above genera are due to differences in the

frequency of chiasma formation in the species. *Datura* has a higher frequency of chiasma formation than *Primula sinensis*. It is therefore to be expected that more complex multiple associations will be formed in *Datura* than in *Primula sinensis*. This suggestion is supported by the fact that certain complicated configurations of chromosomes which require six chiasmata for their occurrence are found in *Datura* but not in *Primula sinensis*.

A statistical count of chromosome numbers in *Datura* and *Solanum* was made by Blakeslee, Belling and Farnham and the Lesleys, respectively. In *Datura* out of 243 pollen mother-cells examined 70% had the normal 24-24 distribution and 30% had 23-25, while 22-26 and 21-27 were only found rarely. In tomato 23-25 was found in 22% of cases and 22-26 in 6% of cases out of 49 second divisions examined. Jørgensen, on the other hand, found great regularity of the 24-24 distribution in his tomato material. A study of the chromosome numbers in pollen grains of triploid *Hyacinthus* has also been made by Belling and by Darlington (see Darlington, 1926).

Meiosis in *Primula sinensis* was found to be fairly regular (Sömme, 1930; Darlington, 1931 c). Non-disjunction of chromosomes was observed and giant cells were sometimes found at the second division. A statistical count of the numbers of chromosomes present at the second division has not been made, but it may be assumed that, like *Datura*, the amount of numerical non-disjunction will not appreciably affect the genetic results. In the case of *Dahlia variabilis* meiosis and numerical disjunction is remarkably regular.

General Characteristics. The increased vegetative vigour of the tetraploid as compared with the diploid is generally noticeable, but *Primula obconica* (Philp, unpub.) is an exception to this rule.

The tetraploid form of *Primula sinensis* is in every respect a coarser and bigger plant than the diploid form from which it arises but otherwise closely resembles it (Gregory, de Winton and Bateson, 1923). In this respect it differs from the tetraploid *Datura* which has characters not common to the diploid form, such as spherical instead of ovate capsules and broader leaves (Blakeslee, Belling and Farnham, 1923). The tetraploid form of *Campanula persicifolia* has a shallower corolla than the diploid form (Gairdner, 1926), and

in *Solanum* Jørgensen (1928) and Sansome (1930) find that the leaf shape of the tetraploid is distinctly different from that of the diploid. Like the tetraploid forms of *Datura* and *Solanum* the tetraploid *P. sinensis* is much less fertile, produces distinctly bigger pollen grains and more bad pollen than the diploid form.

Darlington pointed out in 1928 that there was a correspondence dependent on the chromosome behaviour between the fertility of a diploid and its polyploid derivative.

There is an inverse correlation between the fertility of the

	Seed production of the plant with the lower chromosome number.	Seed production of polyploid derivative.
<i>Raphanus-Brassica</i> (Karpechenko, 1927).	45 per plant	30 per pod
<i>Phleum pratense</i> × <i>P. alpinum</i> (Gregor and Sansome, 1930).	46 in 500,000 flowers, 4 germinated.	over 400 per plant, 90% germination.
<i>Digitalis purpurea</i> × <i>D. ambigua</i> (Buxton and Newton, 1928).	200 seedlings from 2 plants.	400 per capsule.
<i>Nicotiana glutinosa</i> × <i>N. Tabacum</i> Clausen and Goodspeed, 1925).	155 per fruit.	?
<i>Solanum Lycopersicum</i> (Sansome, unpublished).	100 per fruit.	20 per fruit.
<i>Datura Stramonium</i> (Blakeslee, Belling and Farnham, 1923).	352 per fruit.	70 per fruit.
<i>Primula sinensis</i> (Sömme, 1930)	12.6 per fruit.	9.0 per fruit.
<i>Primula sinensis</i> (Darlington, 1931)	32.2 per fruit.	23.2 per fruit.
<i>Campanula persicifolia</i> (Gairdner and Darlington, 1932).	325 per fruit.	150* per fruit.

* In the original paper the number 130 was given in error.

diploid and derivative polyploid. Doubling of the chromosome number in a sterile hybrid generally results in a return to fertility in the polyploid. This is because the chromosomes can pair and behave normally in meiosis giving normal gametes. If the diploid, e.g., *P. Kewensis* ($2x$), is made up of two different sets of chromosomes the plant will be practically sterile since the gametes produced will result from the random assortment of chromosomes in an irregular meiosis. When this diploid becomes tetraploid, however, it will be fertile, since autotetraploidy will take place and give rise to bivalents at metaphase, with

the consequent regular production of viable balanced gametes, e.g., tetraploid *P. Kewensis*. When the diploid is fully fertile the derivative tetraploid will be less fertile, since too much similarity in each group of four chromosomes introduces competition in pairing, therefore non-disjunction will occur, giving rise to unbalanced gametes. The seed production of diploids and tetraploids given above indicates this inverse correlation. As Darlington points out, this explains why allopolyploids are much more widespread in nature than autopolyploids. Any change which differentiates the chromosomes from one another will lead to bivalent formation (allopolyploidy) and to increase in fertility. Such a change will therefore be favoured by selection.

INHERITANCE IN AUTOTETRAPLOIDS

Recently tetraploid inheritance has been studied in *Datura Stramonium*, Blakeslee, Belling and Farnham (1923); *Dahlia variabilis*, Lawrence (1929, 1931 a); *Primula sinensis*, Sömme (1930) and de Winton and Haldane (1931); tomato, Sansome (unpub.). Autotetraploid inheritance with random pairing between four chromosomes, two at a time, followed by regular disjunction to opposite poles of those chromosomes which have paired, gives rise to more complex ratios than in diploids, but (as in diploids) the gametic output obeys the laws of chance and is amenable to mathematical calculation. Muller (1914) and Lawrence (1929) calculated the gametic series to be expected on the above conditions for tetraploids and octoploids. Muller (1914) in considering Gregory's results showed that the assortment of the homologous chromosomes in the autotetraploid must be at random thus leading to a random assortment of factors to the gametes. This hypothesis has been found to explain the known data of autotetraploids.

Using the accepted terminology of Blakeslee, Belling and Farnham, with respect to one factor S, there are five possible types of zygote in the tetraploid, quadruplex SSSS, triplex SSSs, duplex SSss, simplex Ssss and nulliplex ssss, whereas in the diploid there are only three possible types SS, Ss and ss.

If these factors in the tetraploid are assorted at random two at a time, a duplex plant SSss will have a gametic output of 1SS : 4Ss : 1ss.

The possible combinations may be represented diagrammatically thus :—



Such a plant on selfing would give a progeny of (ISS 4Ss 1ss)² or 1SSSS, 8SSSs, 18SSss, 8Ssss, 1sssss.

Where the dominance of a factor over its allelomorph is complete, e.g., short style over long style in *Primula sinensis*, the phenotypic ratio when a duplex plant is selfed is 35 : 1. Back-crossing such a plant to the recessive will give a ratio of 5 : 1.

Table 17 shows the gametic output and zygotic ratios expected in autotetraploid plants. Considering one factor there is only one heterozygote in a diploid, and when dominance is complete, on selfing or intercrossing and back-crossing, it can only give two phenotypic ratios 3 : 1 and 1 : 1. In an autotetraploid, on the other hand, there are three heterozygotes and five possible phenotypic ratios 35 : 1, 11 : 1, 5 : 1, 3 : 1 and 1 : 1. Consequently, in breeding from heterozygous tetraploids, a much larger progeny must be grown in order to obtain the recessive form as compared with that required to be grown from a heterozygous diploid.

Haldane (1930 a) has given a general method for the calculation of the gametic output of any autopolyploid in which the factors are distributed at random to the gametes in the above manner. The generalised formula for the probability of a zygote $A^r a^{2m-r}$ producing a gamete $A^s a^{m-s}$, is

$$\frac{(m!)^2 (2m - r)! r!}{(2m)! (m - s)! (m - r + s)! s! (r - s)!}$$

where r is the number of dominant factors in the zygote, s the number in the gamete and m is the total number of factors in the gamete.

Hence the gametic output of a particular zygote is obtained by calculating the frequency of each possible type of gamete produced.

Tables 18—25 and 28 give the results of experiments with

autotetraploids of *Datura Stramonium* and *inermis*, *Primula sinensis* and *Dahlia variabilis*. (*Dahlia variabilis* is an octoploid,

TABLE 17

Tetrasomic Inheritance of an Allelomorphic Pair (A, a) in Tetraploid Daturas; Formulas for Parents, Gametes, and Offspring (Blakeslee, Belling, and Farnham, 1923)

Parents (Gametes in parentheses).	Mated with	Genetic Types of Offspring.					Ratio $A : a$.	
		A_4 .	A_3a .	A_2a_2 .	Aa_3 .	a_4 .		
$A_4 (A_2)$	{	A_4	I	$\infty : 0$	
		A_3a	I	I	$\infty : 0$	
		A_2a_2	I	4	I	$\infty : 0$	
		Aa_3	I	I	$\infty : 0$	
		a_4	I	$\infty : 0$	
$A_3a (A_2 + Aa)$	{	A_4	I	I	$\infty : 0$	
		A_3a	I	2	I	$\infty : 0$	
		A_2a_2	I	5	5	I	$\infty : 0$	
		Aa_3	I	2	I	$\infty : 0$	
		a_4	I	I	$\infty : 0$	
$A_2a_2 (A_2 + 4 Aa + a_2)$	{	A_4	I	4	I	$\infty : 0$	
		A_3a	I	5	5	I	$\infty : 0$	
		A_2a_2	I	8	18	8	I	35 : I
		Aa_3	I	5	5	I	11 : I
		a_4	I	4	I	5 : I
$Aa_3 (Aa + a_2)$	{	A_4	I	I	$\infty : 0$	
		A_3a	I	2	I	$\infty : 0$
		A_2a_2	I	5	5	I	11 : I
		Aa_3	I	2	I	3 : I
		a_2	I	I	I : I
$a_4 (a_2)$	{	A_4	I	$\infty : 0$	
		A_3a	I	I	$\infty : 0$
		A_2a_2	I	4	I	5 : I
		Aa_3	I	I	I : I
		a_4	I	0 : ∞

but behaves like an autotetraploid with regard to the inheritance of the characters investigated.)

It will be seen that the agreement between expectation, based on the above assumptions. and observation is generally close.

Datura Stramonium. The inheritance of the factor pairs **A — a** for spiny *vs.* spineless capsules and **P — p** for purple *vs.* white flower colour are the most fully investigated characters in *Datura*. Tables 18 and 19 show the breeding data and the expected ratios calculated on the basis of random assortment of the chromosomes.

Table 19*b* shows the breeding data and calculated ratios expected for flower colour in other races. Unfortunately, the individual parents of this race were not very adequately analysed by growing large families of selfed progeny and of back-crosses. It was therefore found necessary to add to the ratio obtained from the cross $P_2P_2 \times P_2P_2$ certain families, containing no whites, which resulted from selfing plants of unknown constitution and which, from the size of the families, could not be expected to contain recessive individuals even if they were duplex. The proportion of purples is then rather high.

Similarly, it was necessary to add certain families containing no whites to the backcross results obtained from the plants of unknown genetic constitution. It is to be expected that no recessives would be present in such small families from a $P_2P_2 \times P_4$ cross. With this addition the proportion of whites is slightly high.

In this race proof of the correctness of the above hypothesis was obtained. One plant 17108(9) selfed gave 151 purple and backcrossed to the recessive gave 66 purple and therefore was either P_4 or P_3p . One of the selfed progeny—plant 1998(16)—selfed gave 479 purple and thus was either P_4 or P_3p . Nineteen of the last progeny were tested by selfing and it was found that 15 gave all purple and 4 gave the ratio 35 : 1. These four plants were therefore P_2P_2 and plants 1998(16) and 17108(9) were P_3p .

It will be noticed from the table that the observed results of the inheritance of spines in *Datura* deviate much more from expectation than do those of flower colour. Where the offspring segregate for spines and spineless there is always an excess of spineless except in the 5 : 1 and 1 : 1 ratios. The most striking deviation is the occurrence of recessives where none is expected (see Table 18, lines 3 and 4). It will be noted also that in the inherit-

TABLE 18
Tetrasomic Inheritance of the Allelomorphic Characters Spiny (A) and Spineless (a) in the Tetraploid Datura (Blakeslee, Belling and Farnham, 1923)

Cross.	Theoretical ratio.	Observed.	Calculated.	No. of families.	Dev. P.E.
A_1 or A_3 \times A_4 or A_2	$\infty A : o a$	1897 A : o a	1897 A : o a	9	—
" " \times A_2a_2 and reciprocal	$\infty A : o a$	439 A : o a	439 A : o a	5	—
" " \times A_1a_3 "	$\infty A : o a$	747 A : 7 a	754 A : o a	9	—
" " \times a_4 "	$\infty A : o a$	257 A : 6 a	263 A : o a	6	—
$A_2a_2 \times A_2a_2$	$35 A : 1 a$	3383 A : 118 a	3403.7 A : 97.3 a	13	$\frac{20.7}{6.56} = 3.155$
" \times A_1a_3 and reciprocal	$11 A : 1 a$	319 A : 32 a	321.7 A : 29.3 a	6	$\frac{2.7}{3.49} = 0.774$
" \times a_4 "	$5 A : 1 a$	518 A : 137 a	545.8 A : 109.2 a	10	$\frac{27.8}{6.43} = 4.323$
$A_1a_3 \times A_1a_3$	$3 A : 1 a$	1337 A : 570 a	1430.2 A : 476.8 a	9	$\frac{93.2}{12.76} = 7.304$
" \times a_4 and reciprocal	$1 A : 1 a$	144 A : 144 a	144 A : 144 a	6	$\frac{0.0}{5.72} = 0.00$
$a_4 \times a_4$	$0 A : \infty a$	0 A : 324 a	0 A : 324 a	2	—

TABLE 19a
Tetrasomic Inheritance of the Allomorphic Characters Purple (P) and White (p) Flower Colour
in the Tetraploid Datura (Blakeslee, Belling and Farnham, 1923)

Cross.	Theoretical ratio.	Observed.	Calculated.	No. of families.	Dev. P.E.
P ₄ or P ₃ p × P ₄ or P ₃ p	∞ P : ∞ p	1201 P : ∞ p	1201 P : ∞ p	5	—
" × P ₂ p ₂ and reciprocal	∞ P : ∞ p	128 P : ∞ p	128 P : ∞ p	3	—
" × P ₁ p ₃ "	∞ P : ∞ p	75 P : ∞ p	75 P : ∞ p	1	—
" × P ₄ "	∞ P : ∞ p	532 P : ∞ p	532 P : ∞ p	6	—
P ₂ p ₂ × P ₂ p ₂	35 P : 1 p	3225 P : 106 p	3238.5 P : 92.5 p	15	$\frac{13.5}{6.39} = 2.113$
" × P ₁ p ₂ and reciprocal	11 P : 1 p	394 P : 42 p	399.6 P : 36.3 p	9	$\frac{5.7}{3.89} = 1.465$
" × P ₄ "	5 P : 1 p	905 P : 179 p	903.3 P : 180.7 p	14	$\frac{1.7}{8.37} = 0.206$
Pp ₃ × P ₁ p ₃	3 P : 1 p	188.3 P : 64.2 p	189.3.7 P : 631.3 p	11	$\frac{10.7}{14.68} = 0.729$
" × P ₄ and reciprocal	1 P : 1 p	292 P : 266 p	279 P : 279 p	11	$\frac{13.0}{7.97} = 1.631$
P ₄ × P ₄	∞ P : ∞ p	∞ P : 563 p	∞ P : 563 p	2	—

TABLE 19b

Cross.	Theoretical ratio.	Observed.	Calculated.	No. of families.	Dev. P.E.
$P_3p \times P_3p$	$\infty P : o p$	1280 $P : o p$	1280 $P : o p$	3	—
$P_3p \times p_4$ and recip.	$\infty P : o p$	160 $P : 1 p$	161 $P : o p$	3	—
$P_2p_2 \times P_2p_2$	$35 P : 1 p$	$6595 + 2604 = 9199 P : 225 p$	$9162.8 P : 261.8$	80	$\frac{36.8}{10.76} = 3.420$
$P_2p_2 \times p_4$ and recip.	$5 P : 1 p$	$515 + 31 = 546 P : 122 p$	$556.7 P : 111.3 p$	31	$\frac{10.7}{6.49} = 1.649$
$Pp_3 \times Pp_3$	$3 P : 1 p$	$7547 P : 2619 p$	$7624.5 P : 2541.5 p$	59	$\frac{102.5}{93.13} = 1.101$
$Pp_3 \times p_4$ and recip.	$1 P : 1 p$	$696 P : 682 p$	$689 P : 689 p$	36	$\frac{7}{12.52} = 0.559$
$p_4 \times p_4$	$o P : \infty p$	$o P : 848 p$	$o P : 848 p$	11	—

ance of flower colour a recessive has been found where none is expected, but this exceptional recessive occurs less frequently than in the case of spineless. These recessives cannot have arisen through numerical non-disjunction since two of the exceptional recessives have each been found to have the correct number of chromosomes (48).

Blakeslee, Belling and Farnham suggested that the recessives may have arisen through an irregularity at the second division of meiosis in such a way that separation takes place between chromosomes carrying unlike factors. This reductional form of second division would produce from an **AAAa** plant, gametes **AA** and **aa**, and the union of two such recessive gametes would produce the exceptional plants (see p. 190). These workers have pointed out the interesting fact that exceptional recessives have occurred in the progeny of the trisomic *Cocklebur*, which has the chromosome carrying spiny or spineless in excess of the diploid number. The trisomic mutant *Poinsettia*, whose extra chromosome contains the factor for flower colour, has never produced exceptional recessives for flower colour. This they conclude is evidence that the chromosome set carrying spiny-spineless is in some way different from that carrying purple-white flower colour.

It will be realised at once that this hypothesis closely approaches that of Bridges and Anderson (1925) and Anderson (1925) previously discussed under linkage. Their evidence from the genetics of *Drosophila* shows that during the first division of meiosis the identical chromatids remain attached to one another at and near the attachment constriction. Since crossing-over between chromatids of different chromosomes may occur at any other point in the chromosome, the resultant pair of chromatids which pass to one pole may be identical genetically only at the attachment constriction, but different throughout the remaining parts (see p. 121). At the second division the chromatids separate from one another in a mitotic fashion, hence near the point of attachment the division will be genetically equational but at other regions it may be reductional or equational. For example, a chromosome carrying a factor **P** pairs with another carrying the allelomorph **p**, and where the locus of **P** and **p** is not close to the attachment

constriction, crossing-over takes place so that one chromosome has chromatids pP and the other Pp . (See Fig. 32.)

At the second division these chromatids separate from one another

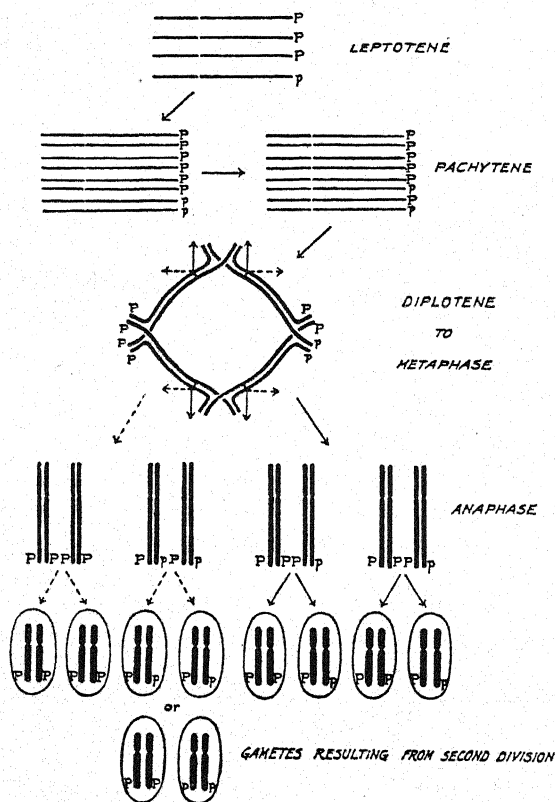


FIG. 32.—Diagram showing random chromosome and random chromatid segregation in a triplex tetraploid.

at random, giving the gametic ratio $1PP:2Pp:1pp$, of which the last is the exceptional type. Therefore a factor whose locus is at least 50 units from the attachment constriction, will segregate on the basis of random association of chromatids. Haldane (1928) and Darlington (1931) have dealt with the consequences of this

TABLE 20

Tetrasomic Inheritance of the Allelomorphic Characters Short style (S) and Long style (s), Green Stigma (G) and Red Stigma (g), Magenta (B) and Red (b), Dominant White (W) and Coloured (w) and Coloured (w), Normal Eye (Q) and "Prinrose Queen" Eye (q), Palm Leaf (P) and Fern Leaf (p) in the Tetraploid Primula sinensis. (After Sömme)

Short style—Long style

Cross.	Expected ratio.	Observed.	Calculated.	Number of families.	
$S_2S_2 \times s_4$	3 : 1	287 S : 45 s	249 S : 83 s	11	$M = 7.9 \frac{Dev.}{M} = 4.8$
	5 : 1		276.7 S : 55.3 s		$M = 6.8 \frac{Dev.}{M} = 1.5$
$S_1S_3 \times S_1S_3$	3 : 1	1000 S : 342 s	1006.5 S : 335.5 s	28	$M = 15.9 \frac{Dev.}{M} = 0.4$
$S_1S_3 \times s_4$	1 : 1	1007 S : 995 s	1001 S : 1001 s	36	$M = 22.4 \frac{Dev.}{M} = 0.3$

TABLE 21
Green stigma—Red stigma

Cross.	Expected ratio.	Observed.	Calculated.	Number of families.	Dev. $\frac{M}{M}$
$G_2g_2 \times G_2g_2$	15 : 1	1659 G : 52 g	1604 G : 107 g	38	$M = 7.0 \frac{M}{M} = 7.9$
	35 : 1		1663.5 G : 47.5 g		$M = 6.9 \frac{M}{M} = 0.7$
$G_2g_2 \times g_4$	3 : 1	1175 G : 223 g	1048.5 G : 349.5 g	30	$M = 16.2 \frac{M}{M} = 7.8$
	5 : 1		1165 G : 233 g		$M = 13.6 \frac{M}{M} = 0.7$
$G_1g_3 \times G_1g_3$	3 : 1	172 G : 59 g	173.2 G : 57.8 g	9	$M = 6.6 \frac{M}{M} = 0.4$
	1 : 1	240 G : 212 g	226 G : 226 g		$M = 10.3 \frac{M}{M} = 1.3$

TABLE 22
Magenta—Red

Cross.	Expected ratio.	Observed.	Calculated.	Number of families.	Dev. $\frac{M}{M}$
$B_2b_2 \times B_2b_2$	35 : 1	205 B : 5 b	204.2 B : 5.8 b	5	$M = 2.4 \frac{M}{M} = 0.3$
$B_2b_2 \times b_4$	5 : 1	272 B : 48 b	266.6 B : 53.4 b	7	$M = 6.7 \frac{M}{M} = 0.8$
$B_1b_3 \times B_1b_3$	3 : 1	264 B : 79 b	257 B : 86 b	6	$M = 8.0 \frac{M}{M} = 0.9$
$B_1b_3 \times b_4$	1 : 1	456 B : 449 b	453.5 B : 453.5 b	25	$M = 14.9 \frac{M}{M} = 0.2$

TABLE 23
Dominant White—Coloured

Cross.	Observed.				Calculated.				Number of families.
	White and tinged white.	Lavender.		Red.	White and tinged white.	Lavender.		Red.	
		Magenta.	Red.			Magenta.	Red.		
$W_2w_2B_2b_2G_4 \times w_4b_4G_4$ $W_2w_2B_2b_2G_4 \times W_2w_2B_2b_2G_4$	18	57	6	4	16.5	55.0	11.0	2.8	4
	351	88	2	1	336.9	97.0	2.7	12.1	9
$W_2w_2B_2b_2G_2g_2 \times W_2w_2B_2b_2G_2g_2$ Expected ratio. 27 : 8 : 1	White and tinged white.	Lavender.		Full colour.	White and tinged white.	Lavender.		Full colour.	
	363 $M = 10.0$ $Dev. = 0.6$ $\frac{Dev.}{M}$	114 $M = 9.2$ $Dev. = 0.5$ $\frac{Dev.}{M}$		15 $M = 3.7$ $Dev. = 0.3$ $\frac{Dev.}{M}$	369.0	109.3		13.7	8
$W_2w_2B_2b_2G_2g_2 \times w_4b_4g_4$ Expected ratio. 1 : 4 : 1	Tinged white.				Tinged white.				
	43 $M = 5.3$ $Dev. = 1.7$ $\frac{Dev.}{M}$	121 $M = 6.8$ $Dev. = 2.0$ $\frac{Dev.}{M}$		38 $M = 5.3$ $Dev. = 0.8$ $\frac{Dev.}{M}$	33.7	134.6		33.7	6

B and G are linked having cross-over percentages of 35.18% on the female side and 34.38% on the male side.

TABLE 24
Normal—"Primrose Queen" Eye

Cross.	Normal eye, long style.	Normal eye, homostyle.	Primrose Queen eye, homostyle.	Number of families.
$Q_2q_2 \times Q_2q_2$ Expected on a 27:8:1 basis.	$(Q_4 + Q_3 + Q_2)$ 158 148.5 $M = 6.0$ Dev. $\frac{Dev.}{M} = 1.6$	(Q_1q_3) 31 43.0 5.8 2.1	(q_4) 8 5.5 2.3 1.0	14
$Q_2q_2 \times q_4$ Expected on a 1:4:1 basis.	(Q_2q_2) 50 17.5 $M = 3.8$ Dev. $\frac{Dev.}{M} = 8.5$	(Q_1q_2) 38 70 4.3 7.4	(q_4) 17 17.5 3.8 0.1	13
$Q_1q_3 \times Q_1q_3$ Expected on a 1:2:1 basis.	35 19.8 $M = 3.9$ Dev. $\frac{Dev.}{M} = 3.9$	31 39.5 4.4 1.5	13 19.8 3.9 3.9	5
$Q_1q_3 \times q_4$ Expected on a 1:1 basis.	8* 0 $M = -$ Dev. $\frac{Dev.}{M} = -$	40 46 4.8 1.3	44 46 4.8 0.4	5

* These eight plants are probably Q_1q_3 overlapping towards the normal condition.

behaviour and shown that chromatid segregation has no effect in diploids but in triploids and higher polyploids it must be considered.

Primula sinensis. The inheritance of six factors and their allelomorphs has been studied in the tetraploid *Primula sinensis* :

- S s short *vs.* long style.
 G g green *vs.* red stigma.
 B b magenta *vs.* red flowers.
 W w Dominant white *vs.* coloured flower.
 Q q normal *vs.* "Primrose Queen" eye.
 P p palm *vs.* fern leaf.

TABLE 25
Palm—Fern Leaf

Cross.	Palm.	Extra lobes.	Fern.	Number of families.
$P_2p_2 \times P_2p_2$. Observed Expected on a 27 : 8 : 1 basis.	293	74	10	9
	282.7	83.8	10.5	
	M = 8.4	7.9	3.2	
	Dev.			
	$\frac{Dev.}{M} = 1.2$	1.2	0.1	
$P_2p_2 \times p_4$. Observed Expected on a 1 : 4 : 1 basis.	27	49	18	6
	15.7	62.6	15.7	
	M = 3.6	3.8	3.6	
	Dev.			
	$\frac{Dev.}{M} = 3.1$	3.6	0.6	
$P_1p_3 \times P_1p_3$. Observed Expected on a 1 : 2 : 1 basis.	92	149	76	15
	79.3	158.5	79.3	
	M = 7.7	8.9	7.7	
	Dev.			
	$\frac{Dev.}{M} = 1.6$	1.1	0.4	
$P_1p_3 \times p_4$. Observed Expected on a 1 : 1 basis.	6*	101	100	10
	—	103.1	103.1	
	M = —	7.2	7.2	
	Dev.			
	$\frac{Dev.}{M} = —$	0.3	0.5	

* These six plants are assumed to be P_1p_3 overlapping to the normal type.

These factors are also known in the diploid and are inherited in the normal 1 : 1 and 3 : 1 ratios of disomic inheritance.

Tables 20—25 summarise the results of the experiments on inheritance of these factors in the tetraploid.

It will be noticed in some cases that in the crosses of the type $A_2a_2 \times a_4$ and $A_2a_2 \times A_2a_2$ the expected results are calculated on two theoretical ratios. One ratio is based on the theory that pairing has taken place in an allosyndetic manner : A with a but not A with A and a with a, followed by random segregation at the second division.

This theory, suggested by Gregory in 1914, gives ratios of 3 : 1

and 15:1 respectively. The other ratio is calculated on the assumption that the chromosomes carrying **A** and **a** pair at random and undergo normal disjunction. The observed results agree more closely with this latter expectation.

Quantitative Expression. In this work some light has also been obtained on the question of the quantitative effect of the factors. Only in the cases of **S.s.** (short *vs.* long style) and **G.g.** (green *vs.* red stigma) was dominance found to be complete, *i.e.*, the simplex form had the phenotypic characteristics of the dominant factor. In the other factors in tetraploid *P. sinensis* the simplex form was only partially dominant in the phenotypic expression, which was intermediate and highly variable. (In diploids **S**, **G**, **B**, **Q** and **P** are completely dominant.)

The simplex form (G_1g_3) has a green stigma but the flower colour is almost as dark as that of the nulliplex form (g_4). This is in contrast to the duplex (G_2g_2) and triplex form (G_3g_1) where the flower colour is lighter. Thus it is concluded that G_1 is dominant over g_3 with respect to stigma colour and is only partially dominant in respect of its effect on flower colour.

Of particular interest is the recessive character "Primrose Queen" eye. The factor for this was found by Gregory (1911) to be in diploids the lowest member of a series of three multiple allelomorphs, *viz.*, "Queen Alexandra" eye (no eye) (Q_1), normal eye (**Q**) and "Primrose Queen" eye (the eye extends over about a third to a half of the petal) (**q**). The recessive factor for "Primrose Queen" not only affects the eye but also the style. Gregory found in diploids that this factor caused genetically long-styled plants to become homostyled and that the single dose of the dominant factor (**Q**) was completely dominant both as regards the effect on the eye and the long style. In tetraploids, however, Q_1 was found to be completely dominant over q_3 regarding the expression of the eye but not as regards the style, *i.e.*, normal eye—homostyled plants were found to be Q_1q_3 . These heterozygotes were liable to vary in expression of the style, especially at the latter part of the flowering season. At that time flowers were produced which were normal-eye long-styled. This is therefore not only an example of the quantitative effect of the factors, but also of the effect of one factor on more

than one character and probably of the physiological effect on the expression of a factor.

An interesting example of interaction of factors is afforded by the factors for dominant white (**W**) and green stigma (**G**). Flowers with a green stigma (**G**) are paler in colour than those with a red stigma (**g**). The effect of **W** is that of inhibiting the production of flower colour in the peripheral parts of the flower. In the presence of **G**, **WW** causes the flower to be white, while **Ww** inhibits colour in the periphery (*i.e.*, there is a tinge of colour round the corolla tube). In the presence of **g**, **WW** allows a dark flush of colour to be produced round the corolla tube (*var.* *Duchess*) and **Ww** permits this colour to be diffuse (*var.* *General Buller*).

In tetraploids there is an increased number of possible combinations of these factors and their interaction and quantitative effects have proved to be troublesome in the classification of the different types of plants. For that reason Table 23 only shows that most of the expected classes have appeared. This condition, as expected, is by no means uncommon in tetraploids, and in one family a range of the phenotypes may be obtained which defies determination of the genotype from the phenotype. Further breeding tests will only reveal the genotype and this process, because of the tetraploid nature of the plants, necessitates the growing of very large progenies, which in many cases is impracticable. In contrast diploids have only three possible genotypes with regard to one pair of factors, and therefore, even when the factor expression differs quantitatively and factor interaction takes place, the possible range of types is less than that in tetraploids. Thus it is seldom necessary to classify diploids by breeding tests. Obviously from a horticultural point of view a much greater number of forms should be obtained from a tetraploid species than from the corresponding diploid species.

A striking example of the quantitative effect of factors was obtained by Lawrence (unpublished) in *Dahlia variabilis*, an allo-octoploid with autotetraploid inheritance of **A B**, two factors for anthocyanin, and **Y I** (yellow) **I** (ivory), two factors for flavones. In the progeny of a cross between two parents of known constitution

there were 8 yellow, 8 ivory and 0 white-flowered plants when there should have been

Yellow.	Ivory.	White.
6YI 2Yi	6yI	2yi

On testing for flavone the following result was found :—

	Yellow-ivory.	Yellow-white.	Ivory.	White.
expected	6	2	6	2
observed	1	7	8	0

Such a result cannot be due to chance. Three of the seven yellow flowers with a white ground gave a faint positive reaction for ivory

TABLE 26

Capsule Volume of Funaria hygrometrica (Wettstein, 1924)

diploid	BB 185.62 (50)	—	—	B × b 97.06 (18)	—	—	bb 57.74 (50)
triploid	BBB 176.91 (5)	—	BB × b 145.77 (12)	—	bb × B 101.31 (14)	—	bbb 59.62 (17)
tetra- ploid	BBBB 242.71 (50)	BB × Bb 228.18 (8)	—	BB × bb 196.64 (9) Bb × Bb 208.92 (50)	—	bb × Bb 124.96 (6)	bbbb 151.35 (50)

flavone (I) while the other four were negative. From these and other results Lawrence concludes that in the presence of Y the I factors cannot exert their full effect. The three yellow-white forms which gave a faint positive reaction for I, were probably I_2i_2 in constitution while the other four were Ii_3 . The single YI form was probably I_3i . It is possible that the material from which the yellow and ivory flavones are manufactured is limited in amount and the Y factors obtain a monopoly. Y and I also interfere with the expression of anthocyanin by the A and B factors.

This interaction of the chemical processes involved sometimes has a disturbing effect upon the ratios and creates difficulty in genetical analysis.

Tables 26 and 27 of capsule volume and form of polyploid *Funaria hygrometrica* (Wettstein, 1924 a) illustrate well the influence of a size factor B upon character expression. The diploid Bb is

intermediate between **BB** and **bb**. **BBb**, **BBbb** and **Bbb** have capsule volumes corresponding to the effect of **B** alone. The nulliplex tetraploid **bbbb** however has a larger volume than expected from the remaining figures. **B** also affects the gametophytic leaf shape,

TABLE 27
Form of Capsule Lid, Breadth : Length

diploid	BB 4.80	—	—	B × b 2.99	—	—	bb 2.63
triploid	BBB 4.52	—	BB × b 3.97	—	bb × B 2.91	—	bbb 2.71
tetra- ploid	BBBB 5.29	BB × Bb 5.13	—	BB × bb 3.04 Bb × Bb 2.75	—	bb × Bb 2.59	bbbb 2.68

and here the effect of **B** is greater than that of **b**, the leaf areas of **BB** plants being 1.91, **bb** 2.88, **Bb** 2.27.

Capsule Colour.

CC	Cc	cc		
orange	yellow-orange	ochre		
<i>lid</i>	<i>lid</i>	<i>lid</i>		
orange	red-ochre	ochre		
CCC	CCc	ccC	ccc *	
orange-red	orange	ochre to rusty	ochre	
<i>lid</i>	<i>lid</i>	<i>lid</i>	<i>lid</i>	
red	dark orange	ochre	ochre	
CCCC	CCCc	CCcc	Cccc	cccc
orange-black-red		yellow-orange	rust-ochre	rusty
<i>lid</i>		<i>lid</i>	<i>lid</i>	<i>lid</i>
black-red		black red	ochre	ochre

As regards capsule volume, the full effect of **B** is not reached even in quadruplex tetraploid, but in the case of **C** for colour of capsule the saturation point is reached between 2-3 **C** factors, since **CCCC**, **CCCc** and **CCcc** have all black-red capsule lids while **CC** and **CCc** have dark orange lids. It will be noticed, however, that not

until the triplex condition is reached does the general capsule colour become dark red, although the lid does so with CCcc.

In the above cases of capsule volume and colour the nulliplex **xxxx** does not resemble the **xx** or **xxx** forms but agrees more with the simplex **Xxxx** or even duplex **XXxx**.

Stern (1928), by means of duplications, was able to breed flies of *Drosophila melanogaster* with increasing numbers of the recessive bobbed genes. Bobbed (**bb**) in the diploid state suppresses the development of hairs on the body of the flies.

By numerous crosses using duplications of **bb** and its allelomorphs, + normal, **bb**¹ a lethal with more intensive effect, and **bb**¹¹, another lethal, Stern was able to show that there was a quantitative effect of these factors upon the development of hairs. To the factors he gives the following numbers as a comparative measure of their influence.

normal	30
Y ^{bb¹}	10
X ^{bb}	8
Y ^{bb¹¹}	4
X ^{bb¹}	2

When the sum of the values of these allelomorphs present in females amounts to 30, the character of hairs is equal to normal, but when less than 30 the bobbed characteristic, e.g., **X**^{bb}, **X**^{bb}, **Y**^{bb¹} = 26 makes its appearance. The factors on other chromosomes also affect the expression of the bobbed factors. This is shown by the fact that a diploid female with **X**^{bb} **X**^{bb} has longer hairs than an intersex with more autosomes than normal.

Dahlia variabilis. Table 28 shows the single factor ratios obtained in *Dahlia variabilis* (the garden Dahlia) by Lawrence (1929, 1931 *a* and unpublished). This species is an allo-octoploid and the results demonstrate that tetrasomic inheritance takes place for the following factors. **A** usually produces pale anthocyanin, **B** usually produces deep anthocyanin, **Y** produces yellow flavone and **I** produces ivory flavone. **Y** and **B** are completely dominant, i.e., the simplex form is as deeply coloured as the quadruplex form. **I** is not dominant in the simplex condition and it is also cumulative in its effect. The

progeny of the cross $Y_3y \times y_4$ gave seven unexpected recessives. These may have arisen from double-reduction.

TABLE 28
Tetrasomic Inheritance in the Octoploid Dahlia variabilis
(Lawrence, unpublished)

Cross.	Number of families.	Observed.		Calculated.		Dev.	Dev. σ
		Dominant.	Recessive.	Dominant.	Recessive.		
$A_3a \times a_4$	4	180	0	180	0	—	—
$A_2a_2 \times A_2a_2$	2	85	1	83.6	2.4	— 1.38	0.91
$A_2a_2 \times a_4$	7	221	44	220.8	44.2	— 0.16	0.02
$Aa_3 \times a_4$	2	99	115	107.0	107.0	+ 8.0	1.09
$a_4 \times a_4$	47	0	2,327	0	2,327	—	—
$B_3b \text{ or } B_4 \times B_2b_2$	2	72	0	72	0	—	—
$B_3b \text{ or } B_4 \times b_4$	1	92	0	92	0	—	—
$B_2b_2 \times b_4$	4	237	44	234.2	46.8	— 2.83	0.45
$Bb_3 \times B_4$	9	309	314	311.5	311.5	+ 2.5	0.20
$b_4 \times b_4$	46	0	2,004	0	2,004	—	—
$Y_3y \times Y_2y_2$	5	444	0	444	0	—	—
$Y_3y \times Yy_3$	3	259	0	259	0	—	—
$Y_3y \times y_4$	4	378	7*	385	0	—	—
$Y_2y_2 \times Y_2y_2$	1	107	3	106.9	3.1	— 0.05	0.02
$Y_2y_2 \times Yy_3$	5	513	50	516.1	46.9	+ 3.09	0.46
$Y_2y_2 \times y_4$	21	708	169	730.8	146.2	+ 22.83	2.11
$Yy_3 \times Yy_3$	7	411	118	396.8	132.2	— 14.25	1.42
$Yy_3 \times y_4$	16	488	472	480.0	480.0	— 8.0	0.51
$y_4 \times y_4$	14	0	558	0	558	—	—
$I_4 \times I_3i$	1	13	0	13.0	0	—	—
$I_4 \times I_2i_2$	2	89	0	89	0	—	—
$I_3i \times I_2i_2$	6	47	1	44.0	4.0	— 3.0	1.57
$I_3i \times Ii_3$	1	4	4	6.0	2.0	+ 2.0	1.63
$I_2i_2 \times I_2i_2$	6	129	35	123.0	41.0	— 6.0	1.09
$I_2i_2 \times Ii_3$	13	175	187	181.0	181.0	+ 6.0	0.63
$Ii_3 \times Ii_3$	4	32	129	40.2	120.8	+ 8.25	1.50

* Recessives arising from double reduction.

LINKAGE IN AUTOTETRAPLOIDS

Linkage in polyploids has been investigated in triploid *Drosophila* and maize and in tetraploid *Primula sinensis* and tomato. With the number of homologous chromosomes greater than two in the sporocytes, greater variation in the assortment of linked factors

is to be expected. For example, in a tetraploid with four homologous chromosomes containing two pairs of allelomorphic factors, there are seven possible types of arrangement of the factors on the chromosomes (Sömme, 1930 and de Winton and Haldane, 1931). If we designate the homologous chromosomes $ABCD$ and the factor pairs $XxYy$ we can have the following different arrangements:—

	<i>A.</i>	<i>B.</i>	<i>C.</i>	<i>D.</i>
1.	XY	xy	xy	xy single coupling.
2.	Xy	xY	xy	xy single repulsion.
3.	Xy	Xy	xY	xY double repulsion.
4.	XY	XY	xy	xy double coupling.
5.	XY	XY	Xy	xy asymmetrical coupling.
6.	xY	Xy	Xy	xy asymmetrical repulsion.
7.	Xy	xY	XY	xy coupling and repulsion.

Since crossing-over occurs during the time the chromosomes are paired the method of pairing of the four chromosomes, two at a time must be considered. With random pairing there are three ways in which these chromosomes $ABCD$ can pair, namely, A with B , A with C and A with D , when in each case, of course, the remaining two chromosomes pair with one another. Disjunction of the chromosomes which have paired therefore leads to six possible different types of gamete with respect to chromosome content— AB , AC , AD , CD , BD and BC .

Thus $\begin{array}{c} A \ C \\ | \ | \\ B \ D \end{array}$ gives the gametes AC , BD , AD , BC .

$\begin{array}{c} A \ B \\ | \ | \\ C \ D \end{array}$ „ „ „ AB , CD , AD , BC .

$\begin{array}{c} A \ B \\ | \ | \\ D \ C \end{array}$ „ „ „ AB , CD , AC , BD .

To consider the effect of crossing-over let us take the case of single repulsion. Assuming that chromosome A contains the factors X and y , and that chromosome B contains the factors x and

Y, then chromosomes *C* and *D* each contain the factors *x* and *y*. In one-third of all the cases *A* will pair with *B* and if crossing-over takes place, then between these factors the gametic series with regard to chromosomes *A* and *B* will be $p \text{ XY} : (1-p) \text{ Xy} : (1-p) \text{ xY} : p \text{ xy}$ where p is the cross-over value. (This is the same as in diploids.) Chromosomes *C* and *D* will pair and disjoin at the same time as chromosomes *A* and *B*. Crossing-over between *C* and *D*, however, will have no genetical effect since they only contain the recessive factors *xy* and the gametic series with regard to these two chromosomes will be $1 \text{ xy} : 1 \text{ xy}$. In each type of gamete containing an *A* or *B* chromosome there will be a *C* or *D* chromosome, *i.e.*, two chromosomes which have paired do not normally enter the same gamete. Thus considering all four chromosomes the gametic series will be:—

$$p \begin{array}{c} \text{XY} \\ \text{xy} \end{array} : (1-p) \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : (1-p) \begin{array}{c} \text{xY} \\ \text{xy} \end{array} : p \begin{array}{c} \text{xy} \\ \text{xy} \end{array}$$

In the remaining two-thirds of cases *A* will pair with *C* or *D* and *B* with *D* or *C*, and in each case crossing-over will have no genetical effect. For each type of pairing the gametic series will be:—

$$\frac{1}{2} \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : \frac{1}{2} \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : \frac{1}{2} \begin{array}{c} \text{xY} \\ \text{xy} \end{array} : \frac{1}{2} \begin{array}{c} \text{xy} \\ \text{xy} \end{array}$$

and adding them we get

$$1 \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : 1 \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : 1 \begin{array}{c} \text{xY} \\ \text{xy} \end{array} : 1 \begin{array}{c} \text{xy} \\ \text{xy} \end{array}$$

This summed with

$$p \begin{array}{c} \text{XY} \\ \text{xy} \end{array} : (1-p) \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : (1-p) \begin{array}{c} \text{xY} \\ \text{xy} \end{array} : p \begin{array}{c} \text{xy} \\ \text{xy} \end{array}$$

gives the total gametic series

$$1 \begin{array}{c} \text{Xy} \\ \text{xY} \end{array} : p \begin{array}{c} \text{XY} \\ \text{xy} \end{array} : (2-p) \begin{array}{c} \text{Xy} \\ \text{xy} \end{array} : (2-p) \begin{array}{c} \text{xY} \\ \text{xy} \end{array} : (1+p) \begin{array}{c} \text{xy} \\ \text{xy} \end{array}$$

When dominance is complete the different types of zygote, quadruplex, triplex, duplex and simplex will be phenotypically indistinguishable. The gametic series may therefore be written $(1+p) \text{ XY} : (2-p) \text{ Xy} : (2-p) \text{ xY} : (1+p) \text{ xy}$. If p and q

represent the cross-over values on the male and female sides respectively, then the zygotic series is:—

$$18 + (1 + p)(1 + q) \mathbf{XY} : 9 - (1 + p)(1 + q) \mathbf{Xy} : \\ 9 - (1 + p)(1 + q) \mathbf{xY} : (1 + p)(1 + q) \mathbf{xy}.$$

TABLE 29
(de Winton and Haldane, 1931)

Type of zygote.	Types of gametes.	Gametes in general.	Gametes, $p = 0$.	Gametes, $p = \frac{1}{2}$.	Gametes in absence of linkage.	Zygotic ratio on selfing.
1. $\mathbf{XY} \cdot (\mathbf{xy})_3$	\mathbf{XY}	$1 - p$	1	1	1	$2 + (1 - p)(1 - q)$
	\mathbf{Xy}	p	0	1	1	$1 - (1 - p)(1 - q)$
	\mathbf{xY}	p	0	1	1	$1 - (1 - p)(1 - q)$
	\mathbf{xy}	$1 - p$	1	1	1	$(1 - p)(1 - q)$
2. $\mathbf{Xy} \cdot \mathbf{xY} \cdot (\mathbf{xy})_2$	\mathbf{XY}	$1 + p$	1	1	1	$18 + (1 + p)(1 + q)$
	\mathbf{Xy}	$2 - p$	2	1	1	$9 - (1 + p)(1 + q)$
	\mathbf{xY}	$2 - p$	2	1	1	$9 - (1 + p)(1 + q)$
	\mathbf{xy}	$1 + p$	1	1	1	$(1 + p)(1 + q)$
3. $\mathbf{XY} \cdot \mathbf{Xy} \cdot (\mathbf{xy})_2$	\mathbf{XY}	$3 - p$	3	5	5	$26 + (1 - p)(1 - q)$
	\mathbf{Xy}	$2 + p$	2	5	5	$9 - (1 - p)(1 - q)$
	\mathbf{xY}	p	0	1	1	$1 - (1 - p)(1 - q)$
	\mathbf{xy}	$1 - p$	1	1	1	$(1 - p)(1 - q)$
4. $(\mathbf{Xy})_2 \cdot \mathbf{xY} \cdot \mathbf{xy}$	\mathbf{XY}	$2 + p$	2	5	5	$26 + pq$
	\mathbf{Xy}	$3 - p$	3	5	5	$9 - pq$
	\mathbf{xY}	$1 - p$	1	1	1	$1 - pq$
	\mathbf{xy}	p	0	1	1	pq
5. $(\mathbf{XY})_2 \cdot (\mathbf{xy})_2$	\mathbf{XY}	$5 - 2p + p^2$	5	17	25	$34 + (1 - p)^2(1 - q)^2$
	\mathbf{Xy}	$2p - p^2$	0	3	5	$1 - (1 - p)^2(1 - q)^2$
	\mathbf{xY}	$2p - p^2$	0	3	5	$1 - (1 - p)^2(1 - q)^2$
	\mathbf{xy}	$1 - 2p + p^2$	1	1	1	$(1 - p)^2(1 - q)^2$
6. $(\mathbf{Xy})_2 \cdot (\mathbf{xY})_2$	\mathbf{XY}	$4 + p^2$	4	17	25	$34 + p^2q^2$
	\mathbf{Xy}	$1 - p^2$	1	3	5	$1 - p^2q^2$
	\mathbf{xY}	$1 - p^2$	1	3	5	$1 - p^2q^2$
	\mathbf{xy}	p^2	0	1	1	p^2q^2
7. $\mathbf{XY} \cdot \mathbf{Xy} \cdot \mathbf{xY} \cdot \mathbf{xy}$	\mathbf{XY}	$8 + p - p^2$	4	33	25	$136 + pq(1 - p)(1 - q)$
	\mathbf{Xy}	$2 - p + p^2$	1	7	5	$4 - pq(1 - p)(1 - q)$
	\mathbf{xY}	$2 - p + p^2$	1	7	5	$4 - pq(1 - p)(1 - q)$
	\mathbf{xy}	$p - p^2$	0	1	1	$pq(1 - p)(1 - q)$

For purposes of calculation it is convenient to put $1 - p = P$, $1 - q = Q$.

The gametic series in double coupling may then be written $4 + P^2 : 1 - P^2 : 1 - P^2 : P^2$, and the expressions for the following zygotic series may be simplified:

Single coupling, $2 + PQ : 1 - PQ : 1 - PQ : PQ$.

Asymmetrical coupling, $26 + PQ : 9 - PQ : 1 - PQ : PQ$.

Double coupling, $34 + P^2Q^2 : 1 - P^2Q^2 : 1 - P^2Q^2 : P^2Q^2$.

Coupling and repulsion, $136 + pqPQ : 4 - pqPQ : 4 - pqPQ : pqPQ$.

The effect of crossing over in the remaining six types of arrangement of the factors may be calculated in a similar fashion and the results are given in Table 29, which is taken from the paper by de Winton and Haldane (1931).

It will be observed that in the cases of double coupling, double repulsion and asymmetrical coupling and repulsion a difference in ratio is to be expected between independent segregation of the factors and 50% of crossing-over. In the diploid and in the other types of linkage in tetraploids, this difference is not observable. This fact may be useful, on some occasion, to decide whether two factors are far apart on the same chromosome or on different non-homologous chromosomes.

It will be realised that several assumptions have been made for the calculation of linkage ratios. It is assumed that (1) chromatid segregation does not take place, (2) non-disjunction of chromosomes does not occur, and (3) only two chromosomes are involved in crossing-over between the factors concerned. The first two phenomena have been dealt with already in connection with the inheritance of single factors. As regards the third assumption, it is probable that in those plants with high chiasma frequency one chromosome does pair with more than one of its homologues in different parts of its length. Hence crossing over between one chromosome and three other homologous chromosomes is possible, but the genetic data from plants have not indicated so far that this is the case. In *Drosophila* triploids, however, Bridges and Anderson and Redfield have observed the results of progressive as well as recurrent cross-overs.

In single coupling in an autotetraploid between three factors **XYZ** de Winton and Haldane point out that progressive crossing-over would produce gametes, and hence progeny, containing these factors in the repulsion phase to a greater extent than in the corresponding diploid.

Thus the factors on the four homologous chromosomes may be represented **X Y Z**. Progressive crossing-over would give the

x y z

x y z

x y z

TABLE 30

Linkage results in tetraploid Primula sinensis. (After de Winton and Haldane, 1931)

SINGLE COUPLING.						
Cross.	Number of families.	SG	Sg	sG	sg	
SG.(sg) ₃ × (sg) ₄	17	204	126	113	193	
Calculated	—	198.5	119.5	119.5	198.5	
(sg) ₄ × SG.(sg) ₃	20	132	89	97	160	
Calculated	—	146	93	93	146	
SG.(sg) ₃ × SG.(sg) ₃	7	179	47	40	27	
Calculated	—	174.4	45.3	45.3	27.9	
SINGLE REPULSION.						
Sg.sG.(sg) ₂ × (sg) ₄	23	126	136	146	102	
Calculated	—	116.9	138.1	138.1	116.9	
(sg) ₄ × Sg.sG.(sg) ₂	14	38	57	60	52	
Calculated	—	47.9	55.6	55.6	47.9	
DOUBLE REPULSION.						
(Sg) ₂ .(sG) ₂ × (sg) ₄	12	124	21	19	0	
Calculated	—	113.3	23.4	23.4	3.9	
(sg) ₄ × (Sg) ₂ .(sG) ₂	2	11	0	1	0	
Calculated	—	8.3	1.7	1.7	0.30	
DOUBLE COUPLING.						
(SG) ₂ .(sg) ₂ × (sg) ₄	6	146	18	13	18	
Calculated	—	142.7	19.8	19.8	12.7	
(sg) ₄ × (SG) ₂ .(sg) ₂	2	81	13	9	17	
Calculated	—	87.5	12.5	12.5	7.5	
(SG) ₂ .(sg) ₂ × (SG) ₂ .(sg) ₂	4	104	3	4	2	
Calculated	—	107.2	2.7	2.7	0.45	
ASYMMETRICAL COUPLING.						
SG.Sg.(sg) ₂ × (sg) ₄	3	26	15	3	5	
Calculated	—	21.4	19.4	3.1	5.1	
SG.sG.(sg) ₂ × (sg) ₄	14	156	9	108	35	
Calculated	—	134.7	19.3	122	32	
(sg) ₄ × SG.sG.(sg) ₂	5	48	7	50	13	
Calculated	—	51.4	7.7	47	12	
SG.sG.(sg) ₂ × SG.sG.(sg) ₂	10	373	7	118	10	
Calculated	—	371.2	9.8	121.6	5.4	
ASYMMETRICAL REPULSION.						
Sg.(sG) ₂ .sg × (sg) ₄	44	422	98	439	70	
Calculated	—	407.5	107	450	64.5	
(sg) ₄ × Sg.(sG) ₂ .sg	10	33	7	38	4	
Calculated	—	32.7	8.3	35.7	5.3	
Sg.(sG) ₂ .sg × Sg.(sG) ₂ .sg	25	847	31	267	7	
Calculated	—	836.8	27.2	283.2	4.8	

chromosomes carrying the factors thus $X y z$ and amongst others

$x Y z$

$x y Z$

$x y z$

the following gametes containing the factors in the repulsion phase would be obtained $X y z$, $X y z$, $x Y z$

$x Y z$ $x y Z$ $x y Z$.

The F_1 of such a plant would therefore contain individuals possessing the factors in the condition of single repulsion, double repulsion and exceptional ones having repulsion of all three factors. The F_2 from these individuals would show up the constitution of those with single repulsion and double repulsion. Until the F_3 was obtained, however, the condition of the factors in the exceptional types would not be shown. The same result would be obtained if non-disjunction of chromosomes occurred after crossing over.

Evidence such as this, involving progressive double crossing-over, has not been observed by de Winton and Haldane, and therefore they adopt the scheme outlined above as being at present approximately in line with the meiotic behaviour of the chromosomes which contain the factors investigated. The close agreement of the calculated figures with the observed result, can be seen in Table 30 constructed from the data of de Winton and Haldane.

These experiments are important from several points of view. They confirm the theory that factors are carried on the chromosomes. When the number of homologous chromosomes is increased the number of allelomorphs of one factor is also increased. Segregation of factors is controlled by the disjunction and behaviour of the chromosomes at meiosis. It should be noted, however, that in *Primula sinensis* non-disjunction or chromatid segregation has not so far been reported to have any effect on segregation of factors. Other species such as *Datura* and *Rubus* exhibit factor segregation explicable on the basis of "double reduction."

The assumption of the purity of the gamete requires to be modified in polyploid inheritance. In tetraploids the gametes are diploid and contain two allelomorphs. For example, a duplex plant S_2s_2 produces gametes of the constitution SS , ss and Ss ; the last type is heterozygous and "impure." The possibility of obtaining pure

lines for several characters in the dominant condition is more remote in tetraploids than in diploids. Artificial or natural selection on a diploid with incomplete dominance comparatively soon effects purity, but in a polyploid the recessives are more protected from the action of selection.

CHAPTER VI

ALLOPOLYPLOIDS

Autosyndesis—Allosyndesis—Genetical Consequences—Shift—Wheat—Oats—Speltoids and Fatuoids—Allopolyploidy and Evolution—Secondary Pairing—Secondary Polyploids.

In an autotetraploid the four homologous chromosomes can pair with one another and assort at random to each pole. This type of pairing—autosyndesis—leads to a definite type of segregation of the heritable characters, which has already been dealt with.

Allopolyploids contain a complement of chromosomes derived from two or more plants of dissimilar origin, and it is upon the degree of similarity between these two or more kinds that the type of pairing and disjunction of the chromosomes and hence the segregation of factors depend.

Autosyndesis and Allosyndesis. Two types of pairing of the chromosomes at meiosis in allopolyploids can take place, namely, autosyndetic and allosyndetic. Thus in an allotetraploid there may be two sets of chromosomes derived from one species and two sets of chromosomes derived from a different species. For simplicity we shall consider only one pair of the corresponding chromosomes from each species and designate them *AA BB*.

If *A* is homologous with *A* and *B* with *B*, and if the *A* chromosomes are not homologous with the *B* chromosomes, then *A* will always pair with *A*, and *B* with *B* to form bivalents at meiosis—autosyndesis.

Allosyndesis takes place if the chromosome *A* pairs with the *B*, *i.e.*, allosyndetic pairing between chromosomes of different phylogeny. Obviously there is sometimes difficulty in deciding whether allosyndesis or autosyndesis is taking place in border line cases—the difficulty arises from the factorial constitution (heterozygosity) and the systematic position of the parental species.

Genetical Consequences. Theoretically the genetical results from autosyndesis and allosyndesis will be different. In the former

where A pairs with A and B with B , the gametes will contain AB . The succeeding generation will contain $AABB$ like the parent and will behave like a diploid regarding the segregation of single factors. Allosyndesis, on the other hand, will give a gametic output of $1AA : 2AB : 1BB$, and consequently a greater range in the chromosomal constitution of the progeny. By such a method of pairing the parental type $AABB$ will be recovered only 1 in 16 times on selfing such a plant—the chromosomes behave in separation like the segregation of two factors.

With constant autosyndesis segregation of factors only occurs when the ultimate parent was heterozygous. It follows, therefore, that forms with constant autosyndesis will generally breed true.

In the intergeneric F_1 hybrid ($2n = 18$) between *Raphanus* and *Brassica*, Karpechenko (1927 a, b, 1928) the nine *Raphanus* chromosomes are greatly differentiated from the nine *Brassica* chromosomes. No pairing takes place between the two sets. The F_2 tetraploids which result from the fusion of unreduced gametes (p. 174), are perfectly fertile and breed true. The F_2 plants are of the constitution $RRBB$ where R and B represent the *Raphanus* and *Brassica* sets of chromosomes respectively. Autosyndetic pairing takes place and only gametes of the constitution RB are formed. Some of the plants in the parental species were heterozygous, and Karpechenko found that in the tetraploid offspring segregation took place for those factors in which either the *Brassica* or *Raphanus* species were heterozygous.

Allopolyploids, in which autosyndesis is the prevalent method of pairing, are of widespread occurrence. Difficulty is experienced sometimes in identifying them as polyploids and not as normal diploids. The methods of attacking the problem resolve themselves into two main systems; one is of a genetical nature, and the other cytological. Comparison with related forms often provides an indication that a form under investigation is an allopolyploid. The related species of commercial wheat and oats may have chromosome numbers of 14, 28 or 42, while the commercial stocks have 42 chromosomes in the somatic cells. This indicates that the cultivated varieties are hexaploids ($6x = 42$). Bivalents are formed at meiosis and their breeding behaviour is like that of a diploid with

peculiar complications such as the presence of polymeric and duplicate factors and with the production of off-type forms in an unusual manner (fatuoids and speltoids, see p. 224). It is interesting to note in passing that Gregor and Sansome have synthesised an artificial hexaploid *Phleum* (see p. 351), the origin of which in some respects is presumably analogous to that of the commercial wheat and oats. *Spartina Townsendii* is another species in the Gramineæ which in some degree resembles the above forms as to its mode of origin.

Spartina Townsendii is an allopolyploid which has originated in nature. From its characters it is concluded that it arose by hybridisation of the species *S. alterniflora* and *S. stricta*. Huskins (1930) finds that the somatic chromosome number of *S. alterniflora* is 70, that of *S. stricta* is 56, while that of *S. Townsendii* is 126. He also finds that bivalents are formed in meiosis of *S. Townsendii*. This species is very vigorous, fertile, and breeds practically true. It is therefore concluded that *S. Townsendii* is an allopolyploid hybrid analogous to *Primula Kewensis*, having arisen through doubling of the chromosome number of a sterile hybrid between *S. alterniflora* and *S. stricta*. The formation of bivalents and its true breeding nature indicate that autosyndesis takes place.

Besides the evolutionary importance of producing a new true breeding form by inter-crossing two species whose chromosomes are non-homologous, the process of autosyndesis enables a number of valuable physiological properties, dependent upon heterozygosity, to be retained. Polymeric factors are characteristic of allopolyploids (see p. 218). If two species hybridise they will probably be somewhat closely related and will have similar factors in common. The polyploid hybrid will contain these factors and they will segregate independently of one another. One can visualise the position where one pair of factors is heterozygous and the other pair is dominant and homozygous for the same character. The segregation of the heterozygous pair in the polyploid will not affect the particular character expression, since it will be controlled by the other pair of dominants. Hence an allopolyploid may be heterozygous for several factors and yet on account of autosyndesis breed true. It is well known that heterozygosity is

often accompanied by increased vigour (so-called hybrid vigour or heterosis). Hence the allopolyploid may be more vigorous and more adaptable to various conditions. Obviously the allopolyploid may be heterozygous for lethal factors and be weaker than normal, but selection will eliminate these types (cf. Åkerman (1922)). The increase in chromosome number alone generally gives greater vegetative vigour to the plant in comparison with its diploid relative. There are several examples where this heterozygosity of the allopolyploid may be inferred. The general phenomenon is known as "shift."

"Shift." Autosynthesis in a group of chromosomes carrying the factors for type of prickles in the allotetraploid *Rubus* (RT₄) led to its breeding true for the parental *R. rusticanus* type of prickles, while the other parental *R. thyrsiger* type was never recovered (see p. 214).

This behaviour closely resembles the observations of "shift" in crosses between tetraploid *Triticum* species by Biffen (1916) and Engledow (1920 a). Darlington (1928) considers that the phenomenon of "shift" in polyploid cereals is an example of the result of autosynthesis. Engledow (1920 a, 1923) crossed *Triticum polonicum* ($4x = 28$) with *T. durum* (Kubanka) ($4x = 28$), and found simple 1 : 2 : 1 segregation in the F₂ for the long and short glume characters of *polonicum* and *durum* respectively. The typical glume length of *polonicum*, however, was never recovered in the F₂ and later generations, although the hybrids had longer glumes than *durum*. It was therefore concluded that there had been a "shift" in the expression of the character.

Darlington supposes that the two parental species differ in more than one factor governing glume length. Simple segregation of the principal factor takes place giving the parental types as regards this factor. A partially or wholly dominant factor D is carried by each of two dissimilar chromosomes of *T. durum* and is transmitted to the complement of the F₁. These two chromosomes, although unlike, undergo autosynthesis, and therefore no segregation for the factor D occurs. Regular autosynthesis in these chromosomes will always give the same constitution as the F₁, namely, DDdd. Therefore the constitution dddd necessary for the expression of the

polonicum length of glume will not be recovered. If however allosyndesis occasionally occurs in the pairing of these two chromosomes the shift will break down and the parental types will be recovered.

The work of Biffen (1916), while illustrating shift, also shows how such a type of pairing may persist with extreme regularity. In the progeny of a grey-chaffed Rivet, *Triticum turgidum*, crossed with a white-chaffed *T. polonicum*, he found no segregation in chaff colour. From 20 F_1 plants succeeding generations were grown up to F_6 totalling almost 100,000 plants. All these plants showed uniform chaff colour resembling that of the normally recessive white-chaffed parent. Darlington considers that a single dominant factor **W** in *T. polonicum* inhibits the grey chaff colour of *T. turgidum* (**ww**), and that autosyndesis in the F_1 (**WWww**) and later generations results in their breeding true.

Shift was also found by Vavilov and Jakuskhina (1925) in the cross *Triticum persicum* Vav. var. *fuliginosum* Zhuk. \times *T. durum* var. *hordeiforme*. The beak-like tooth to the glume, like that of *T. durum*, was never recovered among 566 F_2 and 4,000 F_3 plants.

Another possible example of shift is the suppression and accentuation of characters, observed by Backhouse (1918) in the cross of *T. polonicum* with Kubanka.

Autosyndesis and Allosyndesis in one Organism. In the above case it will be seen that the heterozygosity of the plant is unsuspected until autosyndesis is interrupted by rare allosyndetic pairing. That allosyndesis occurs regularly between some chromosomes in some allopolyploids is shown by the behaviour of *Primula Kewensis* and of the hybrid ($2n = 28$) between *Fragaria bracteata* and *F. Helleri*, both of which have 14 chromosomes in the somatic tissue (Ichijima (1926, 1930) and Yarnell (1931).

In both these forms the cytology indicates that autosyndesis is most prevalent but in *P. Kewensis* (hybrid of *P. floribunda* and *P. verticillata*) one quadrivalent is found at meiosis together with the expected bivalents. This quadrivalent indicates that one pair of *floribunda* chromosomes is homologous at least in part with one pair of *verticillata* chromosomes. Allosyndesis also occurs in the *Fragaria* hybrid where one quadrivalent is found together with ten bivalents.

In *Primula Kewensis* no genetical segregation was found to correspond with the random pairing between the chromosomes of *floribunda* and *verticillata* (in the quadrivalent). In *Fragaria bracteata* \times *F. Helleri*, however, Yarnell (1931) found that the F_1 plants were heterozygous for pink flower colour. The parent *F. bracteata* had white flowers. The F_2 plants, seven in number, were all pink-flowered. Further breeding analysis showed that the genetic constitution of these seven F_2 plants was :—

	PPPP	PPp	PPpp	Pppp	pppp
observed	0	1	2	4	0
expected	0.19	1.55	3.5	1.55	0.19

The numbers are small but indicate that the F_1 plant was of the constitution PPpp and that random pairing had occurred among the two pairs of chromosomes which carried the factors respectively for pink and white flower colours from *F. Helleri* and from *F. bracteata*.

An important example showing non-segregation of factors borne on chromosomes with autosyndetic pairing, and segregation of factors borne on chromosomes which pair allosyndetically and at random, is that of the *Rubus* hybrid RT_4 ($2n = 28$).

It will be remembered that RT_4 arose from the union of an unreduced egg of *Rubus rusticanus inermis* ($2n = 14$) with a normal pollen grain of *R. thyrsiger* ($2n = 28$) (see p. 176). *R. rusticanus inermis* is a form of *R. rusticanus* without prickles. The type *R. rusticanus* however develops prickles along the angles of the furrowed stem and does not develop acicles or pricklets. *R. thyrsiger* develops prickles which are not confined to the angles of the stem. RT_4 developed its prickles directly and they were confined to the angles of the stem as in *R. rusticanus*. The selfed progeny of RT_4 consisted of prickled and unprickled plants. All the prickled plants behaved in the same way as RT_4 with regard to development of prickles, *i.e.*, *rusticanus* type of prickles on the mature growth. This implies that the F_1 plants of RT_4 each have one or more chromosomes represented two or more times in the complement derived from *R. rusticanus*. Further, the fact that RT_4 breeds true for this character (the *thyrsiger* type of prickles is

never recovered) shows that in RT_4 these chromosomes pair autosyndetically.

The chromosomes containing the factors for the production of prickles, however, do not pair autosyndetically. The results obtained by Crane and Darlington (1932) are given below, along with the expectation on the various hypotheses. Obviously expectation based on random chromatid segregation or double reduction (see p. 189) fits most closely with the observed results, and Crane is of the opinion that this is the best explanation.

TABLE 31
(After Crane and Darlington, 1932)

	Prickled.	Unprickled.
F₂.		
Observed numbers	835	37
Autosyndesis expectation ($\infty : 0$)	872	0
Random assortment expectation (35 : 1)	847.8	24.2
Allosyndesis expectation (15 : 1)	817.5	54.5
Random chromatid expectation (20.78 : 1)	832.0	40.0
F₁ back crossed to recessive.		
Observed numbers	33	10
Autosyndesis expectation ($\infty : 0$)	43	0
Random assortment expectation (5 : 1)	35.8	7.2
Allosyndesis expectation (3 : 1)	32.3	10.7
Random chromatid expectation (3.67 : 1)	33.8	9.2

The cytology of RT_4 also shows that different types of pairing take place. At first metaphase bivalents, trivalents and quadrivalents are formed but only three or four chromosomes of the series are capable of forming trivalents and quadrivalents. Univalents often lag and divide on the equator at anaphase as a result of irregularity in the disjunction of the trivalents and quadrivalents.

The genetic behaviour of RT_4 , which has been outlined above, shows that it contains two sets of *rusticanus* chromosomes. These have undoubtedly been contributed to it by an unreduced *rusticanus* gamete.

The case of an allopolyploid whose chromosome sets are all different has also to be considered. Thus in a tetraploid hybrid between two allotetraploid species, *e.g.*, cherry, or between a diploid and hexaploid species, *e.g.*, plum, the four sets of chromosomes may be designated *AB/CD*. Autosynensis, allosynensis or even random

Autosynensis.	Allosynensis.
Gametic output $SS_I : S_I S : Ss_I : ss_I$ <i>i.e.</i> , $S \ s$ $3 : 1$ Zygotic output $S \ s$ $15 : 1$	$Ss : S_I S_I : S_I S : Ss_I$ or $Ss : SS_I : s_I S : s_I S_I$ <i>i.e.</i> , no segregation or $S \ s$ $3 : 1$ no segregation or $S \ s$ $15 : 1$
Random pairing.	Random chromatid pairing.
Gametic output $1SS_I : \left\{ \begin{array}{l} 1 Ss \\ 1 S_I S_I \\ 1 Ss_I \\ 1 S_I S \end{array} \right\} : 1ss_I$ <i>i.e.</i> , $S \ s$ $5 : 1$ Zygotic output $S \ s$ $35 : 1$	$S \ s$ $22 : 6$ $S \ s$ $20 \cdot 78 : 1$

pairing may take place. Further, the affinity of the chromosomes for one another may be such that *B* can pair with *A* or *C*, and *C* with *B* or *D*, but *A* may be unable to pair with *D*. Here *B* and *C* form a link between *A* and *D*, and if *B* and *C* pair, *A* and *D* may be left unpaired. Darlington considers that this is possibly the explanation of the occurrence of unpaired chromosomes in tetraploid cherries.

It follows that in certain allopolyploids where different types of pairing may take place, the genetic results may be very difficult to analyse. In an allopolyploid where all the sets of chromosomes are of different kinds, the possibilities and complexity of types of pairing are greatly increased. It is not surprising, therefore, that interspecific polyploid hybrids normally give complex segregation. To recognise the particular type of segregation is often well nigh impossible.

We have seen in *Fragaria*, *Rubus* and *P. Kewensis* that chromosomes may pair in different ways, and also examples of the resulting genetical segregation. Unfortunately segregation of factors in forms with both allosyndetic and autosyndetic pairing or with autosyndetic and random pairing has not yet been extensively studied.

If we have a plant of the chromosome constitution *AABB* carrying a pair of factors *Ss* on *AA* and a pair *S₁s₁* on *BB* the segregation expected on the three types of pairing will be as shown in the Table on the opposite page.

The gametic and zygotic outputs of plants of a constitution such as *Ssss* or *SSSS* may be similarly calculated by the reader. Obviously therefore the inheritance of characters in an allopolyploid may be comparatively simple, viz., *sssS* with autosyndesis, or highly complicated, viz., *SSSS* with autosyndesis and occasional allosyndesis.

WHEAT AND OATS

The four small grain crops, wheat, oats, barley and rye have the basic chromosome number 7. Cereal barleys and rye are diploids with 14 somatic chromosomes, but wheat and oats occur as diploids, tetraploids and hexaploids. The diploid oat species *Avena brevis*, *A. strigosa*, *A. nuda brevis* and *A. Wiestii* are not of great agricultural value. The diploid wheat *Triticum monococcum* and the tetraploids *T. polonicum*, *T. dicoccum*, *T. persicum* and *T. dicoccoides* are also of very limited economic value, but there are some important agricultural varieties of the tetraploids species *T. durum* and *T. turgidum*. The species of greatest economic value are the hexaploids *T. vulgare*, *T. compactum*, *A. sativa* and *A. byzantina*.

In this group, however, are also the relatively unimportant species *T. spelta*, *A. fatua* and *A. sterilis*.

It is evident that polyploidy has played an important part in the evolution of the wheat and oat species of economic value. The following evidence shows that they are allopolyploids. Constant autosyndesis in an allopolyploid with bivalent formation would give ordinary diploid segregation if the chromosomes were heterozygous for a pair of allelomorphic factors. It is significant therefore that in polyploid wheat and oats only bivalents are regularly formed at meiosis and genetically they generally behave like diploids giving 3 : 1 or 1 : 2 : 1 F_2 ratios and 1 : 1 back cross ratios. The frequency of duplicate and triplicate factors governing the inheritance of certain characters in the hexaploids also provides evidence that they are allopolyploids, resulting from the hybridisation of different species carrying similar factors affecting these characters. Duplicate factors may arise in a diploid by parallel gene mutations or duplication of parts of chromosomes, but the explanation that the similar factors have been brought into the hexaploid by the different diploid parental species is more feasible. The common occurrence of duplicate factors in hexaploid oats and wheat is in marked contrast to the diploids barley and rye where they are relatively rare. Demonstration of this fact is provided in Table 32, where the type of inheritance is shown for seven characters common to oats, wheat and barley. For these characters there are seven cases of duplicate or triplicate factors in oats, ten in wheat and only four in barley.

Allopolyploidy and hence duplicate and polymeric factors have provided these hexaploids with a distinct advantage physiologically over the diploid species. For example, it is desirable from the point of view of the welfare of the plant and the species, as well as from the economic point of view, that homozygous recessive lethal forms should occur very rarely. Thus a hexaploid heterozygous for three duplicate factors for chlorophyll production will only produce 1 albino in every 64 of its progeny. Further recessive lethal mutations will rarely show in a polymeric hexaploid as compared with in a diploid. (For mutation rate in the different species of *Avena* and *Triticum* see Stadler, 1929.) A typical example of this is the rare

TABLE 32

Factors controlling inheritance of some Characters common to Oats, Wheat and Barley

Oats.	Wheat.	Barley.
<p>(1) B black b white</p> <p>(2) G grey g white</p> <p>(3) Y yellow y white</p> <p>(4) B₁B₂ black b b₂ white (B factors cumulative and independent)</p> <p>(5) B.G. black b.G. grey b.g. white (B epistatic to G.)</p> <p>(6) B₁B₂G. black b₁b₂G grey bb.g white (B factors independent and epistatic to G)</p> <p>(7) B.G.Y. black b.G.Y. grey b.g.Y. yellow b.g.y. white (B epistatic to G and Y) (G Y)</p> <p>(8) RY₁Y₂, RY₁Y₂, RY₁Y₂, RY₁Y₂ red, rY₁Y₂, rY₁Y₂, rY₁Y₂ yellow, ry₁ry₂ white (R epistatic to Y factors, Y factors independent)</p>	<p>GRAIN COLOUR.</p> <p>(19) R₁ red r₁ white</p> <p>(20) R₂ red r₂ white</p> <p>(21) R₃ red r₃ white</p> <p>(22) R₁R₂, R₁R₃, R₂R₃ red r₁r₂, r₁r₃, r₂r₃ white (R factors cumulative and independent)</p> <p>(23) R₁R₂R₃ red r₁r₂r₃ white (R factors cumulative and independent)</p> <p>(24) P₁P₂ purple p.p₂ white (P factors independent—in 4 species—requires confirmation)</p>	<p>(45) B black or purple b yellow or white</p> <p>(46) Bl blue bl yellow</p> <p>(47) A.B violet-brown, Ab blue, aB brown, ab yellow</p>

Cases of duplicate factors are underlined.

TABLE 32—continued

Oats.	Wheat.	Barley.
	<p>GLUME COLOUR</p> <p>(25) B black b yellow (26) Br₁ brown br₁ yellow (27) Br₂ brown br₂ yellow (28) Br₁ Br₂ dark brown br₁br₂ yellow (Br factors cumulative and independent) (29) B.Br black b.Br brown b.br yellow (B epistatic to Br)</p>	<p>(48) B. black b. white (49) B.P. black b.P. purple bp white (B epistatic to P) (50) P₁P₂ dark purple P₁P₂, p₁P₂ light purple p₁p₂ white</p>
	<p>PUBESCENCE</p> <p>Glume.</p> <p>(30) P pubescent p glabrous (31) P₁ fully pubescent P₂ half pubescent p glabrous (multiple allelomorphs) (32) P₁P₂ pubescent p₁p₂ glabrous</p>	<p>Rachilla and Glume.</p> <p>(51) P long unbranched pubescent p short unbranched pubescent.</p>
<p>Glume.</p> <p>(9) P pubescent p glabrous (10) P₁P₂ " p₁p₂ " (P factors independent)</p> <p>Back of Grain.</p> <p>(11) P₁P₂ pubescent lower and upper grain, P₁P₂ pubescent lower and glabrous upper grain, p₁P₂, p₁p₂, both grains glabrous (P₁ and P₂ complementary) (12) P₁P₂ pubescent p₁p₂ glabrous (P factors independent)</p> <p>Base of Grain.</p> <p>(13) G glabrous g pubescent (14) P₁P₂ pubescent p₁p₂ glabrous (P factors independent)</p>		

HEAD TYPE

- (15) O open panicle o side panicle
 (16) O_1O_2 open panicle o_1o_2 side panicle
 (17) $O_1O_2O_3$ open panicle, $o_1o_2o_3$ side panicle
 (O factors independent and cumulative)

- (33) C compact c lax
 (34) CL compact cL lax cl subcompact
 (35) CL_1L_2 compact, CL_1L_2 less compact, cL_1L_2 lax
 (C incompletely epistatic to L_1 and L_2 , L_1 and L_2 independent) and cumulative

- (52) D dense d lax
 (53) L lax l dense

AWNS

- (36) L awnless l awned
 (37) L_1 awnless, L_2 half awned, l awned (multiple allelomorphs)
 (38) A_1A_2 awned a_1a_2 awnless
 (A cumulative and independent)
 (39) L_1L_2 awnless, L_1l_2 , l_1L_2 , l_1l_2 awned

- (54) A awned a awnless
 (55) L awnless l hooded
 (56) H hooded h awned
 (57) ihA awnless, ihA hooded ihA awned

(I = inhibitor of hoods and awns)
 (H = hoods—epistatic to A)
 (A = awned)

- (58) Hs hooded, HS hoods partly suppressed, hs awned, HS awns partially suppressed

- (59) AKS reduced hooded, AKs hooded, AKS, aKS awnless, AKs, aKS, aks awned

(S = inhibitor of awns epistatic to A or K, not completely dominant to AK)

- (60) C_1C_2 hooded, c_1c_2 awnless, C_1 and C_2 complementary

- (61) $A_1A_2A_3$ awned $a_1a_2a_3$ awnless

(A factors independent)

- (62) $A_1A_2A_3A_4$ awned $a_1a_2a_3a_4$ awnless
 (A factors independent)

Cases of duplicate factors are underlined.

TABLE 32—continued

Oats.	Wheat.	Barley.
	HABIT	
(40) S_1S_2 spring	s winter	(63) S spring s winter
(41) S_1S_2 spring	s_1s_2 winter	(64) W_1 spring, W_1 winter, w_1 , w_1 spring (1 inhibitor of W)
(42) Is spring	is winter	
CHLOROPHYLL DEVELOPMENT		
(18) $G_1G_2G_3$ green $g_1g_2g_3$ lutescens (G factors independent)	(43) G_1G_2 green g_1g_2 albino (G factors independent—4 th species)	(65) G_1 green g_1 albino
	(44) $G_1G_2G_3$ green $g_1g_2g_3$ albino (G factors independent)	(66) G_2 " g_2 "
		(67) G_3 " g_3 "
		(68) G_4 " g_4 "
		(69) Gr " gr variegated
		(70) G_1 " g_1 light green
		(71) GG_1 green, gG_1 striped green, ggr albino (G epistatic to G_1)
		(72) Y green y light yellow
		(73) X_1 " x_1 xantha (yellow-in- viable)
		(74) X_2 " x_2 xantha (yellow-in- viable)
		(75) C_1 " c_1 chlorina (whitish- yellow—later green)
		(76) C_2 " c_2 super-chlorina (whitish yellow—later green)
		(77) V_1 " v_1 virescent (white—later green)
		(78) V_2 " v_2 virescent (white—later green)
		(79) Z_1 " z_1 zwerg (0-10° C. yellow, 20° C. green, but sterile,
		(80) Z_2 " z_2 zwerg (0-10° C. yellow, 20° C. green, but sterile)
		(81) L " l lutescens (green—later yellow—in-viable)

Cases of duplicate factors are underlined.

occurrence of albinos in hexaploid wheat and oats and the relatively frequent occurrence of albinos in diploid barley (see Table 32). Albinism has only been found once in hexaploid wheat (Smith and Harrington, 1929) and once in hexaploid oats (Philp, unpub.). In wheat it was inherited on a three-factor basis, while in oats the inheritance has not been fully investigated, but more than one factor is concerned. Another example is that of a black Swedish oat having only one factor for black, and which through mutation gave 10–20 white grains per kilo—an undesirable mixture. By crossing this black variety with an inferior black variety having two factors for black, another good variety with two factors for black was obtained which gave practically no white grains (Åkerman,

Åkerman (18), 1922. Arciszewski (35), 1924. Ausborn (26), (27), 1924. Biffen (19)–(23), (25)–(27), (30), (36), 1905 *a*, (45), (48), (52), 1906; (48), (52), 1907; (30), 1916. Blaringhem (51), 1909, 1921 *a*; (55), 1921 *b*, 1922. Caporn (2), (6), 1918 *a*; (24), 1918 *b*. Clark (19)–(23), (26), (27), (39), 1924. Collins (79), 1927. Cooper (42), 1923. Engledow (25), 1914; (51), 1920 *b*; (54), 1924. Fraser (8), (14), 1919. Gaines (1), (19)–(23), (36), (64), 1917. Garber (1), 1922 *a*; (15), 1922 *b*. Garber, Giddings and Hoover (1), 1928. Garber and Quisenberry (1), 1928. Griffiee (48), 1925. Hallqvist (73), (74), 1923; (65)–(68), (76)–(81), 1924. Hara (65), 1929. Harrington (19)–(23), (26), (27), (38), 1922. Harrington and Aamodt (19)–(23), 1923. Hayes and Aamodt (36), 1923. Hayes, Griffiee, Stevenson and Lunden (1), 1928. Hayes and Harlan (52), 1920. Hayes and Robertson (19)–(23), 1924. Hayes, Stakman, Griffiee and Christensen (48), 1923. Henkemeyer (26), (27), (30), (36), 1915. Howard and Howard (19)–(23), (26), (27), (30), (32), (38), 1912; (30), (32), (38), 1915. Kajanus (30), (36), 1911; (36), 1913 *b*; (19)–(23), (30), (34), (36), 1918 *a*, (36) 1918 *b*; (26), (27), (30), (34), (36), 1923 *a* and *b*; (41), 1927. Kajanus and Berg (47), 1924. Kalt (65), 1916. Kezer and Boyack (26), (27), (30), (36), (55), 1918. Kiessling (70), 1918 *a*; (71), 1918 *b*. Lathouwers (19)–(23), (26), (27), 1924. Love and Craig (5), (12), 1918 *a*; (4), (9), (10), 1918 *b*; (19)–(23), (28), (36), 1919 *a*; (19)–(23), 1924. Malinowski (19)–(23), (28), (30), (36), 1914. Mall (26), (27), 1912. Mayer-Gmelin (19)–(23), (26), (27), (30), 1917. Meunissier (36), 1918. Meurman (1), (4), 1926. Meyer (19)–(23), (26)–(28), (30), (36), 1925. Miyake and Imai (46), (53), (60)–(62), 1922. Miyazawa (72), 1921. Nilsson-Ehle (10), (15)–(17), 1908; (1)–(4), (7), (15)–(17), (19)–(23), (26)–(28), (33), (35), 1909; (19)–(23), (26)–(28), 1911 *a*; (19)–(23), 1911 *b*; (65), 1913; (31), (37), 1920; (65)–(67), (73)–(75), 1922. Nilsson-Leissner (30), (36), (41), 1925. Norton (1), 1907. Odland (1), (15), 1928. Olson, Schafer, McCall and Hill (40), 1920. Park (58), 1923. Quisenberry (1), (17), 1926. Schiemann (51), (63), 1923; (63), 1925. Smith and Harrington (43), (44), 1929. Sö (69), 1921. Stoll (30), 1910. Straus (26), (27), (30), (36), 1914. Surface (5), (11), (13), 1916 *a* and *b*. Takahasi (63), 1924. Thatcher (55), 1912. Tschermak (48), 1901; (1), (45), (49), (55)–(57), see Fruwirth, 1923. Ubisch (51), (52), 1916; (45), (50), (52), (59), 1919; (59), 1923. Vavilov and Jakushkina (19)–(23), (29), (36), 1925. Vestergaard (65), 1914; (51), 1915. Wiebe (65), 1924. Wilson (1), 1904; (36), 1907. Zinn and Surface (1), 1917.

1921 b). If the rate of mutation in this new two factor black variety was the same as in the single factor black variety, only one white grain would appear in every 100,000,000. An undesirable feature of polymeric factors is that where recessive lethal mutations take place which are cumulative in their effect, the plant may survive and yet be adversely affected in its growth.

SPELToids AND FATUoids

In cultivated hexaploid wheat, *Triticum vulgare* Hort. ($2n = 42$) and oats, *Avena sativa* L. ($2n = 42$) unbalanced chromosomal forms have been found as mutants. One class with a chromosome deficiency is called the B type, and another with a chromosome in excess is called the C type. A third type, A, has the normal chromosome number.

The three mutant types are morphologically identical both in wheat and oats. The wheat mutants resemble *T. Spelta* L., and are called speltoids. The oat mutants are like *A. fatua* L., and are called fatuoids.

The speltoids differ from the parental type in having lax ears, thick keeled glumes which can only be pulled away from the grain with difficulty, and by the presence of awns. The fatuoid oat differs from the normal parental variety in 3 main characters of the grain—articulation, pubescence and awn development. In each case the group of speltoid or fatuoid characters remain completely linked in their genetical behaviour. Generally, these mutants appear first of all in the heterozygous form, which is intermediate between the normal and the homozygous mutant. Frequently they occur as chimæras in wheat (Åkerman, 1927), and one such case has been reported in oats by Huskins (1928 b).

The genetical behaviour of speltoids is very complicated. The literature on this subject has been summarised by Kajanus (1927) and Watkins (1930). Fatuoids, on the other hand, are simpler in their genetical behaviour. The earlier literature on fatuoids has been dealt with by Stanton, Coffman and Wiebe (1926), Huskins (1927), and by Jones (1930).

A Type. Heterozygous fatuoid or speltoid mutants on selfing give in their progeny homozygous mutants, intermediate heterozygotes

and normals in the ratio of approximately 1 : 2 : 1. All these classes of segregates have the normal chromosome number 42.

Winge (1924) suggested that the hexaploid *T. vulgare* had 21 chromosomes in its gametes which consisted of 3 sets of 7 chromosomes. Further, he supposed that the corresponding chromosomes in each set differed from one another only in a minor degree. Thus a chromosome *A* from one set had corresponding chromosomes *B* and *C* in the other two sets, and *A*, *B* and *C* differed from one another very slightly. (Huskins—see later—in adopting this hypothesis, attributes the slight dissimilarity between the *B* and *C* chromosomes to the hybrid origin of the hexaploid species. Winge implies that it is due to very slight differentiation of the chromosomes following direct triplication of the chromosomes of a single diploid species.) *B* is taken to be carrying the speltoid factors and *C* the normal factors which are epistatic to the speltoid factors. Considering only this group of chromosomes, normal *T. vulgare* would have the

formula represented by $\frac{ABC}{ABC}$.

Owing to the close similarity between the *B* and *C* chromosomes, Winge assumed that occasionally the *B* pairs with *C* (allosyndesis) instead of normally with *B* (autsyndesis) and so gives rise to the gametes *ABB* and *ACC*. The gamete *ABB* uniting with a normal gamete *ABC* would therefore give rise to a heterozygous speltoid

$\frac{ABB}{ABC}$. This heterozygote would give in the next generation,

normals, heterozygous speltoids and homozygous speltoids $\frac{ABB}{ABB}$ in

the ratio 1 : 2 : 1. In support of this hypothesis Winge observed a trivalent and a univalent in an *A* type heterozygous speltoid with 42 chromosomes. These he considered were the three *B* chromosomes paired and the *C* chromosome unpaired. In a homozygous speltoid of the same strain also having 42 chromosomes he found indications of four chromosomes being associated, presumably the four *B* chromosomes.

Huskins (1927, 1928 *a*, *b*) found that a characteristic feature of the cytology of the *A* type heterozygous fatuids and speltoids

was the formation of a trivalent while in the homozygous mutant form of the A type a quadrivalent frequently occurred. He also found that the normal segregates from a heterozygote showed greater irregularity in meiosis than the normals of a pure line. This is probably associated with the higher percentage of bad pollen produced by normal segregates as compared with a cultivated pure line. Heterozygous and homozygous fatuoids also produced more bad pollen than their normal sister plants. Huskins suggests from this evidence that the slight deficiency of the fatuoid classes which he and other workers have observed is due to differential elimination of fatuoid gametes.

The genetical evidence obtained by Watkins and Cory (1931) of a small percentage of allosyndesis in wheat may be regarded as evidence in favour of the hypothesis that A type fatuoids and speltoids arise as a result of abnormal pairing between the B and C chromosomes.

If this hypothesis is correct, then not only does it represent a case of the breakdown of a process of constant autosyndesis (equivalent to the breakdown of shift), but also a case of the effect of chromosomal unbalance; the heterozygote may be denoted as $6x - 1 + 1$.

The old view that fatuoids arose through natural crossing between *A. sativa* and *A. fatua* is quite untenable, since besides the occurrence of fatuoids as chimæras on normal plants, other characters such as grain colour and delayed germination have not been transmitted from *A. fatua* along with the fatuoid complex.

The chromosomal explanation of the origin of A type fatuoids and speltoids, however, is not universally accepted. Several workers have believed that the fatuoids differ from the normal only by a single factor difference. Nilsson-Ehle (1921 *a*) is of the opinion that fatuoids arise as a result of a complex gene mutation involving a group of very closely linked factors taking place in one germ cell of the normal plant. This latter view has been widely accepted.

Jones (1930) found a mutant which was phenotypically like a heterozygous fatuoid. This intermediate fatuoid type bred true, and genetically it behaved like a true fatuoid. It only differed from the normal in this particular set of characters which behaved as a single unit in inheritance. A similar type was reported by

Huskins to have occurred in another variety. In the F₄ of a cross, Red Algerian \times Golden Rain, Jones found another type which he calls "sub-fatuid" or "semi-steriloid." Again this type behaves genetically like a true fatuid. Jones holds the view that A type fatuids arise through gene mutation in the C chromosome. The loss of the C chromosome in the B type heterozygotes (see later) he regards as equivalent to a loss mutation thus unmasking the fatuid characters carried by the B chromosomes. He therefore considers that the different heterozygous mutants have arisen through mutations of different degrees of complexity occurring in the C chromosome. Huskins suggested that the true breeding intermediate fatuid forms might have arisen by gene mutation or deficiency mutation or by crossing-over between "semi-homologous" chromosomes. In connection with the latter suggestion Jones points out that if the B chromosome pairs with the C chromosome to give rise to the heterozygous A type fatuid, it might be expected that the intermediate fatuid type would occur in some definite percentage frequency in the progeny of an A type heterozygous fatuid. No evidence of this has been obtained by Jones.

From a cytological study of A type fatuids Nishiyama (1931) concludes that the meiotic irregularities need not necessarily be a result of the fatuid constitution of the plants. Further, he obtained forty-one chromosome normal and fatuid plants as well as forty-one chromosome heterozygous fatuids (see p. 229). He points out, however, that of the forty-one chromosome types those having lost the C chromosome occurred in a higher proportion. This, he states, may be due to the C chromosome showing meiotic irregularity more often than the other chromosomes, or to a limited number of chromosomes taking part in these irregularities. There is also the possibility, however, that the products of the meiotic irregularities involving the C chromosome may be more viable than those involving other chromosomes. It appears therefore that this evidence is not in great opposition to the chromosomal aberration hypothesis.

A similar line of argument to that of Jones may be advanced against the origin of the A type speltoids on the chromosome hypothesis. In addition to the speltoid mutants there are so-called

partial mutants from the beardless normal, namely, half-bearded normal, bearded normal and beardless speltoid. The characters bearded and speltoid are completely linked, and crossing-over in the A type heterozygous speltoid rarely, if ever, occurs. (Nilsson-Ehle, 1927 *et al.*) This is contrary to Winge's (1924) suggestion that the partial mutants arise through crossing-over between the *B* and *C* chromosomes. It is possible, however, that when *B* and *C* pair crossing-over may not occur within the speltoid or fatuoid complexes: see Jones (1932) and Philp (1932). Perhaps very rare and particular cross-overs in other regions of these chromosomes may lead to the production of the partial mutants.

The only exception to complete linkage between the characters bearded and speltoid, apart from species crosses (Watkins, 1928), is that obtained by Nilsson-Ehle (1927), from a cross, bearded normal \times beardless speltoid. In F_2 and F_3 the cross-over value between bearded and speltoid was 27%. The question therefore arises as to why the A type mutant arising through pairing of the *B* and *C* chromosomes with no crossing-over continues to give no crossing-over in later generations, whilst the partial mutant if produced through pairing of the *B* and *C* chromosomes with crossing-over, continues to give crossing-over in subsequent generations!

Nilsson-Ehle considers that these mutants arise through loss mutation. Owing to their linkage behaviour he regards the two factors bearded and speltoid as lying some distance apart on the chromosome. He supposes that a complex mutation takes place involving not only these two factors but also the factors lying between them, thus preventing crossing-over.

The mutant beardless speltoid, he considers, arises through mutation of the single factor bearded and therefore crossing-over is possible.

Since the cross-over percentage between bearded and speltoid is about 27% and between half-bearded and speltoid is about 36% he believes that the factor for half-bearded lies further from the speltoid factor than the bearded factor. Since no crossing-over can occur between bearded and half-bearded these factors behave genetically like multiple allelomorphs. Watkins (1930) thinks that this indicates that these two factors influence the amount of crossing-over.

B and C Types. From the hypothesis by which he attempted to explain the origin and genetical behaviour of A type speltoids Winge also postulated the occurrence of speltoids with an unbalanced chromosome number $\left(\frac{ABo}{ABC}\right)$ heterozygotes, $\left(\frac{ABo}{ABB}\right)$ and $\left(\frac{ABBB}{ABB}\right)$ homozygotes.

Huskins (1927, 1928 *a, b*) found heterozygous speltoids and heterozygous fatuoids having either 41, 42 or 43 chromosomes. Those with the normal number 42 were of the A type. The 41 chromosome plants were the B type and the 43 chromosome plants were the C type. The heterozygous fatuoids with 41 chromosomes gave ratios varying from 1:5 to 1:10 normals to heterozygotes plus a few dwarf sterile homozygous fatuoids. In this respect they correspond to the B type speltoids. Similarly, the B type of heterozygous speltoid was found to have 41 chromosomes. The dwarf and sterile homozygous fatuoid segregates contained only 40 chromosomes.

In one strain of fatuoids Huskins obtained a ratio of approximately 1:1 normals to heterozygotes together with a few dwarf sterile homozygous fatuoids. Two heterozygotes of this, the C type, were examined; one had 43 chromosomes and the other had 41 chromosomes. C type heterozygous speltoids were also found to have 43 chromosomes. The dwarf and sterile homozygous fatuoid and homozygous speltoid segregates had 44 chromosomes. Normal segregates of both B and C types had the normal chromosome number 42.

In explaining these results Huskins uses Winge's formula.

B type heterozygotes are represented by $\frac{ABo}{ABC}$ and the 40 chromosome dwarf homozygotes resulting from them by $\frac{ABo}{ABo}$.

The 43 chromosome C type heterozygotes are denoted by $\frac{ABCB}{ABC}$

and the 44 chromosome dwarf homozygous segregates by $\frac{ABCB}{ABCB}$.

The 41 chromosome B type heterozygotes characteristically formed 20 bivalents and 1 univalent at first metaphase. Very frequently the split halves of the univalent at first anaphase, are not included in the daughter nuclei. This is regarded as the primary feature controlling the progeny ratios which are also influenced by selective elimination of unbalanced gametes and zygotes. Meiosis of the 40 chromosome dwarf sterile fatuoids was completely irregular.

C type heterozygous speltoids usually had the 43 chromosomes arranged as 20 bivalents and 1 trivalent. Huskins suggests that probably as a result of the method of pairing and disjunction, gametes with 21 chromosomes are formed more often than gametes with 22 chromosomes, thus affecting the ratios. The ratio is further modified by the selective elimination of unbalanced gametes and zygotes. The occurrence of a heterozygous fatuoid having 41 chromosomes in the progeny of a C type substantiates Nilsson-Ehle's statement that C types sometimes give rise to B types. The dwarf sterile homozygous fatuoids with 40 chromosomes have somewhat irregular meiosis. At first metaphase 22 bivalents, or 20 bivalents and one quadrivalent are formed, but pollen degeneration takes place at a later stage.

Håkansson (1930 b, 1931) also observed that B and C type heterozygous speltoids had 41 and 43 chromosomes respectively, and Müntzing (1930 c) also found a speltoid mutant having 43 chromosomes.

Among the progeny of the cross *T. vulgare* var. Marquis \times *T. compactum*, Vasiljev (1929) found a heterozygous speltoid with 41 chromosomes, i.e., B type. Its normal segregates had 42 chromosomes and the homozygous fatuoid segregates had 40 chromosomes. The ratio of the three classes suggests that it is also of the B type. (Philipschenko, 1929.)

The ratio given by heterozygous fatuoids with 41 chromosomes, studied by Nishiyama (1931), was 0.1 normal : 1.5 heterozygote : 1 dwarf sterile homozygous fatuoid. This is different from Huskin's strain, which gave 1 : 5-10 : few dwarf and sterile. Possibly this is due to differences between the two races in the viability of the unbalanced gametes or certation between the gametes with 20 and 21 chromosomes.

Nishiyama also draws attention to an interesting point concerning the balance of the *B* and *C* chromosomes or groups of factors in the formulæ used for the *C* types of fatuids. In the heterozygotes of the *B* type the proportion of *C* to *B* is 1 : 2, which is the same in the homozygous fatuids of the *C* type. This indicates that the phenotype of the *C* type homozygous fatuids should approach that of a heterozygote. This may actually be the case but it has never been reported. If, on the other hand, the *C* type homozygous fatuids are phenotypically true fatuids the formulæ based on Huskin's chromosome hypothesis and Jones' mutation hypothesis $\frac{ABCB}{ABCB}$ and $\frac{ABCC_2}{ABCC_2}$ respectively seem less convincing.

These chromosomal mutants in oats and wheat therefore illustrate that the loss or gain of a chromosome in a polyploid has less effect on the viability of the plant as compared with a diploid. They also show the effect of chromosomal unbalance on the phenotype. This is of particular interest in this case because it permits the production of some characters typical of another species. It is also important in that it demonstrates their allopolyploid nature. Further, they show the effect of chromosomal unbalance in the type of ratios the heterozygotes produce.

The explanation on the chromosomal basis with regard to the *B* and *C* types of fatuids and speltoids seems to be beyond dispute, but there appears to be some doubt concerning the origin of the *A* types.

Throughout the literature on speltoids there is evidence of great variation in the ratios obtained and of the occurrence of aberrant types. Unfortunately, some workers have not allowed for the effect of winter-killing, which vitiates the results. Moreover, natural crossing in these strains takes place fairly frequently as a result of their pollen sterility, especially in those plants with abnormal chromosome number, and many of the aberrant types may have arisen in this way. It is therefore difficult to be certain about the results which do not appear to fit in with the chromosome hypothesis. Moreover, as Huskins has pointed out, these strains are cytologically irregular—deficiency of parts of chromosomes, segmental interchange and crossing-over between the *B* and *C*

chromosomes may take place, all of which add to the general complexity of the problem. In this way the genetical ratios may become modified and more complicated. In addition, it is possible that the *A* chromosome may contain factors similar to those of the *C* chromosome.

Before a complete explanation of the origin and genetic behaviour of these mutants can be given it is obvious that a strictly controlled cytogenetic study of the aberrant types must be made.

Allopolyploidy and Evolution. The evolutionary importance of allopolyploidy cannot be over-emphasised. The realisation that such forms are prevalent has changed the genetical outlook on many problems. We have already touched upon the subject of hybrid vigour, and here attention should be drawn to the phylogenetic viewpoint.

Obviously the parental species of *Primula Kewensis* had a common origin, and since differentiation one from the other, their chromosomes have undergone translocation, inversion and interchange. The same applies to the tetraploid *Fragaria* and other polyploids. Genetical material may have altered to such an extent that the chromatin parts formerly homologous are now non-homologous. The appearance in these hybrids of a quadrivalent indicates that differentiation of chromosomes has not proceeded equally among all the chromosomes. This, of course, is to be expected.

In allopolyploids of long standing there is greater probability that autosyndesis will take place since the presence of more than two homologous chromosomes will reduce fertility (see p. 181). It is, therefore, almost a constant feature of wild polyploids that they are allo- and not autopolyploids.

For similar reasons in allopolyploids as in structural hybrids, the results of any differentiation of chromosomes or of their genetic material will be less affected by natural selection than in diploids. There may therefore be difficulty in determining the original diploid progenitors of an allopolyploid of long standing.

Study of meiosis alone in an allopolyploid whose ancestry is unknown does not help very much in this direction. Under these circumstances it is difficult to determine which type of pairing is

taking place. Meiosis of hybrids between an allopolyploid and other species, preferably diploid species, however, provides this evidence. For example, Ljungdahl (1924) found that the hybrid between the polyploid *Papaver striatocarpum* ($2n = 70$) and the diploid *P. nudicaule* ($2n = 14$) had 42 chromosomes which paired to form twenty-one bivalents. Clearly seven *nudicaule* chromosomes paired with seven *striatocarpum* chromosomes (allosyndesis) and the remaining twenty-eight *striatocarpum* chromosomes paired among themselves (autosyndesis). Thus it may be deduced that a diploid ancestor of *P. striatocarpum*, if not identical with *P. nudicaule*, was very closely related to it. Further, *P. striatocarpum* probably had two other diploid ancestors which were closely related and probably of common ancestry. In such hybrids pairing among all the chromosomes does not always occur; very often allosyndesis occurs and the rest of the chromosomes remain unpaired. *Papaver somniferum* ($2n = 22$) \times *P. orientale* ($2n = 42$) gives a hybrid with 32 chromosomes. Ljungdahl (1922) found that eleven bivalents and ten univalents were formed at meiosis, and it is considered that allosyndesis had taken place between the *somniferum* and *orientale* chromosomes while the remainder of the *orientale* chromosomes remain unpaired. Again it is concluded that *P. orientale* is an allopolyploid, one of whose ancestors is closely related phylogenetically to *P. somniferum*. Similar examples to this are to be found in *Nicotiana* (see p. 316).

Secondary Pairing. A cytological phenomenon known as "secondary pairing" is of great assistance in determining the distant relationships between the different sets of chromosomes in allopolyploids and hence their parentage. Further, it has provided an explanation of the cause of the complexity in genetic segregation in certain cases.

Secondary pairing has only been observed in polyploids having small chromosomes, and it consists of groups of bivalents lying close together at first and at second metaphase. This is not due to chiasma formation, but is considered to be a generalised attraction analogous to that of the homologous pairs of chromosomes at metaphase in mitosis. The attraction is taken to indicate some slight degree of similarity between the chromosomes concerned.

Secondary pairing was first clearly shown by Kuwada (1910), and has been observed by Ishikawa (1911), Rybin (1927), Crane and Darlington (1927), Meurman (1929), Lawrence (1929, 1931 *a, b, c*), Darlington and Moffett (1930), and Moffett (1931). It is discussed in detail by Darlington (1931 *a*) and Lawrence (1931 *c*).

In RT_4 and in the parent tetraploid species *Rubus thyrsiger* secondary pairing occurs (Crane and Darlington, 1927). This shows that there is some similarity between the chromosome sets of *R. thyrsiger*, and hence confirms the genetical evidence of autosyndesis in RT_4 .

Secondary Polyploids. Cytological studies of the *Pomoideæ* by Darlington and Moffett (1930) and Moffett (1931) where multiple association of chromosomes and secondary pairing were observed are of great importance, especially with regard to their conclusions.

The basic chromosome number of *Pyrus* is 17. Diploid varieties of apples with 34 somatic chromosomes and triploid varieties with 51 somatic chromosomes occur in cultivation. In meiosis of diploids Darlington and Moffett found that seventeen bivalents were usually formed and that secondary pairing also occurred. The degree of secondary pairing was variable. Generally nine bivalents formed three groups of three, and eight bivalents formed four groups of four. In isolated cases this form of grouping was found complete in a cell, *i.e.*, seven groups of chromosomes when seventeen would be expected if no secondary pairing had taken place. Trivalents were usually formed in triploids, but associations of from four to nine chromosomes occurred, the association of nine chromosomes, however, being rare.

They conclude that secondary pairing in the diploids is evidence of similarity of certain chromosomes within the sets, but the degree of similarity is insufficient to allow of autosyndesis. Multiple associations of chromosomes in the triploids confirms this view. They consider that the third set of chromosomes make a bridge between the secondarily associated bivalents of the diploid, indicating that autosyndesis occurs within each of the supposed three haploid sets. They therefore conclude that the diploid has really only seven types of chromosomes; three are represented six times and four are represented four times, *i.e.*, it is a trebly hexasomic tetraploid.

The haploid chromosome complement of the diploid apple may be represented thus :—

AAA
BBB
CCC
DD
EE
FF
GG

The derived series of polyploids in the *Pomoideæ* ($2n = 34, 51, 68$) they regard as secondary polyploids having a primary basic chromosome number of seven, the number seventeen being a secondary basic number.

In support of these conclusions they quote the following evidence. Among natural seedlings of the triploid apple variety, Bramley's Seedling ($2n = 51$) (almost certainly their male parents were diploid varieties) those having 41 chromosomes were most frequent. From a normal triploid with 51 chromosomes it would be expected that those plants having 25 or $26 + 17$, *i.e.*, 42 or 43 chromosomes, would be most frequent among the progeny. The number 41, however, happens to be the sum of the primary haploid number 7 and the secondary diploid number 34. Thus they suggest that the 41 chromosome seedlings predominate because of their chromosome balance; they have obtained the primary balance of 7 and the secondary balance of 17.

Further support of this hypothesis is provided by the fact that certain types of somatic chromosomes can be recognised to be represented in the expected number of times. Moffett (1931) has made a cytological study of a large number of the *Pomoideæ*, and found that they all agree with the conclusions arrived at from the study of the apples.

Darlington and Moffett point out that *Rosa*, *Rubus*, *Geum*, *Fragaria* and *Potentilla* have the basic number seven, and they suggest that the production of this secondary basic number has been a definite evolutionary step towards producing the *Pomoideæ*.

It is not surprising that the cytological complexity of the apple

should be reflected in its genetic behaviour. This is shown to be the case with regard to its behaviour concerning incompatibility. Table 2 shows that fewer varieties of apples are self-incompatible than in either hexaploid plums or diploid cherries. It also shows that the frequency of both self and cross incompatibility in apples, plums and cherries increases as the cytological complexity decreases. Reference to the method of inheritance of incompatibility in diploids will illustrate why this result is to be expected (see p. 21).

The general genetic behaviour of diploid and hexaploid *Prunus* species and the apple may be compared in order to demonstrate the correlation between degree of cytological complexity and degree of genetical complexity. In diploid plums, cherries and peaches, variation in most of the characters so far studied is discontinuous and distinct. Crane (1921) and Connors (1919, 1922.)

Our colleague, Mr. Crane, has made a prolonged genetic study of cherries, hexaploid plums and apples. He informs us that in hexaploid plums, variation is much less discontinuous and less distinct than in diploid species of *Prunus*. In apples, inheritance is more complex than in hexaploid plums. A few characters are discontinuous, but many show almost complete intergradation from one extreme to the other.

Conclusions. The outstanding feature of allopolyploids is that their genetic behaviour depends on the type of chromosome pairing at meiosis, which may be autosyndetic, allosyndetic, or free pairing. Pairing in turn depends on the relationships of the chromosomes, and hence on the ancestry of the allopolyploid. Variation in the degree of relationship of the chromosomes in an allopolyploid results in much variation in type of pairing, and hence in very complex genetic segregation.

CHAPTER VII

EUPLOIDS AND ANEUPLOIDS

Triploids—Primary, Secondary and Tertiary Trisomics—Trisomic Inheritance
—Balance—Haploids.

TRIPLOIDS

Origin. Triploids may be produced experimentally by intercrossing diploids and tetraploids. They occur in nature through the mating of gametes containing $2x$ and x chromosomes respectively. Thus, triploids have been found among normal diploid plants in tomato (Lesley and Mann, 1925 ; Lesley, 1928), *Tulipa* (Newton, 1926 ; Newton and Darlington, 1929 ; de Mol, 1928, 1929), *Hyacinthus* (de Mol, 1927 *a, b* ; Darlington, 1929 *b*), *Aconitum* wild species (Darlington, unpublished), *Narcissus* (Nagao, 1929), *Pomoideæ* (Darlington and Moffett, 1930 ; Moffett, 1931), and in many other genera. These have arisen presumably from a diploid plant through the production of a gamete with the unreduced number of chromosomes. The morphology of triploids, like tetraploids, is usually similar to the related diploid, but the habit is more vigorous. Earlier workers emphasised this difference by designating the triploid and tetraploid forms of a species with the names *semi-gigas* and *gigas* respectively. There are a few examples, such as *Raphanus-Brassica*, *Primula Kewensis* and *Rubus*, where the triploid shows qualitative differences from the diploid and tetraploid form. These differences arise from the interaction of factors of dissimilar phylogeny.

It is useful for the purposes of genetic discussion to make a distinction between triploids which have arisen by crossing two plants of different phylogeny and those which have arisen through the crossing of plants of similar origin. The first class of triploids, having three sets of chromosomes, of which at least one is distinct from the other two, may be called allotriploids. The second class

with all three sets of chromosomes homologous may be called autotriploids.

Usually the cross $4x \times 2x$ is more productive than the reciprocal cross $2x \times 4x$. For example, the diploid forms of *Primula sinensis*, *Datura Stramonium*, *Solanum Lycopersicum*, and *Campanula persicifolia*, when used as females in crosses with the tetraploid forms, set no seed. On the other hand, the crosses *Nicotiana glutinosa* ($2n = 24$) \times *N. Tabacum purpurea* ($2n = 48$), *Rubus rusticanus inermis* ($2n = 14$) \times *R. thyrsiger* ($2n = 28$) and *Phleum pratense* ($2n = 14$) \times *P. alpinum* ($2n = 28$) are fertile and produce triploids.

The reciprocal cross $4x \times 2x$ has given rise to most of the experimentally produced triploids, *Primula sinensis* (Sömme, 1930, de Winton and Haldane, 1931), *Datura* (Blakeslee, Belling and Farnham, 1923), *Solanum Lycopersicum* (Lesley, 1928, Sansome, unpub.), *Campanula persicifolia* (Gairdner, 1926) and *Primula malacoides* (Philp, unpub.).

The fertility of the cross, $4x \times 2x$, is from 0.5% to 20% of the normal cross, $2x \times 2x$ (cf. Lesley and Lesley, 1930; McClintock and Hill, 1931; Sömme, 1930; Buchholz and Blakeslee, 1929).

There are probably two main causes underlying the greater sterility of the cross, $2x \times 4x$, as compared with the reciprocal. In *Datura* the pollen tubes carrying $2x$ chromosomes burst soon after pollination of a $2x$ style (Buchholz and Blakeslee, 1929). In *Primula sinensis* $2x$ pollen grains show greatly reduced germination (about 2%). Those which do germinate have no directional properties, as in incompatible pollinations in Gramineæ and *Tulipa* (Sansome, unpub.).

The other cause of sterility in this cross is the reaction of the $2x$ tissue of the mother plant with the $4x$ tissue of the endosperm and $3x$ embryo. The normal balance in a hybrid, diploid \times diploid is, of course, mother plant tissue $2x$, endosperm $3x$ and embryo $2x$ (cf. Watkins, 1932).

It is noteworthy that the majority of successful crosses of the nature $2x \times 4x$, have been between species. This might be expected for the following reason: If we designate the chromosomes of one species used as the female as $2x$ and of the other used as male as

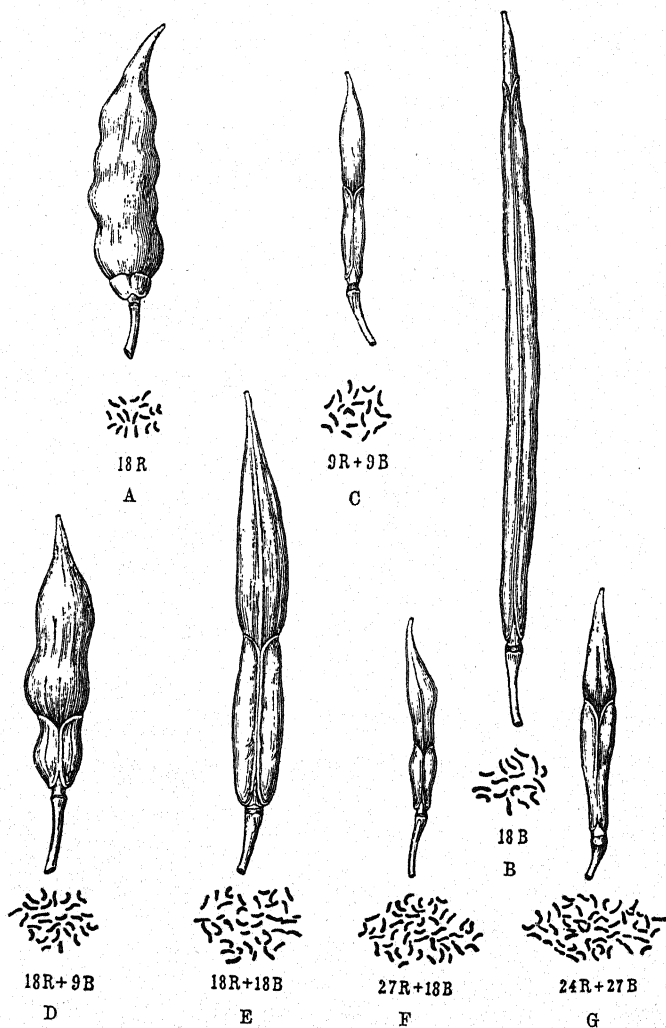


FIG. 33.—Pods, somatic plates of chromosomes and formulæ for *Raphanus* (A), *Brassica* (B), diploid (C), triploid (D), tetraploid (E), pentaploid (F), and hypohexaploid (G) hybrids.
(Karpechenko, 1928.)

$4x^1$, then the mother plant tissue is $2x$, the hybrid endosperm is $2x + 2x^1$ and the hybrid embryo is $x + 2x^1$. This is more similar to the normal chromosomal ratio of mother, endosperm and embryo. In the reciprocal and more fertile cross the ratio is: — mother, $4x$: endosperm, $4x^1 + x$: embryo, $2x^1 + x$.

When the triploid results from the hybridisation of plants with differing characters, the expression of these characters is sometimes of interest. For example, *P. Kewensis* ($4x = 36$), backcrossed to one of its parents *P. floribunda* ($2x = 18$) gave two plants approximately tetraploid and three plants approximately triploid. All five plants had the thick covering of hair characteristic of *P. floribunda* which is not present in *P. Kewensis*. It is suggested that *P. floribunda* has contributed one set of chromosomes to form the triploids and two sets to form the tetraploids. Therefore in the triploids there would be two sets of *floribunda* to one of *verticillata*, and in the tetraploids three sets of *floribunda* to one of *verticillata* (Newton and Pellew, 1929).

Figure 33 from Karpechenko (1928) illustrates the remarkable behaviour of the hybrids of *Raphanus* and *Brassica*. The sterile F_1 hybrid contains nine chromosomes of *Raphanus* (R) and nine of *Brassica* (B) (see p. 173). According to the different ratios of the R:B chromosomes in derivatives, Karpechenko (1927, 1928) observed proportional variation in the characteristic shape of the siliqua of the two genera.

Similar striking examples may be found in *Rubus rusticanus inermis* \times *R. thyrsiger* (Crane and Darlington, 1927), and in *Funaria hygrometrica* (Wettstein, 1924 a).

Cytology. Cytological examination of triploids in *Tulipa* and *Hyacinthus* and *Primula sinensis* (Dark, 1931) confirms the general conclusions derived from genetical and cytological data of other plants. It has been found that trivalents are formed more frequently by the longer than by the shorter chromosomes of *Tulipa* (Newton and Darlington, 1927), *Zea Mays* (McClintock and Hill, 1931), *Hyacinthus* (Belling, 1927 a, 1929; Darlington, 1929 b). If metaphase pairing depends on the retention of chiasmata formed at the preceding prophase in meiosis, the minimum number of chiasmata required to form a trivalent is two as compared with one chiasma

required for bivalent formation. If the frequency of chiasma formation is proportional to the length (but see Fig. 21) it is expected that more trivalents will be formed by the larger chromosomes, cf. Darlington and Mather (in press—"Cytologia") and Stone and Mather (in press—"Cytologia").

The formation of trivalents leads to regular numerical non-disjunction of one of the three homologous chromosomes. Distribution at the poles of a reduction division will therefore be represented by a binomial curve with a mean and mode midway between the x and $2x$ number of chromosomes. Thus, in a triploid plant of *Datura* or tomato with the basic number $x = 12$ the maximum number of chromosomes at one pole will be 24 and the minimum number 12, due to the 2-1 disjunction of each trivalent. It is expected that the greatest number of gametes with a particular chromosome number will be those with 18 chromosomes, but see p. 244.

When a trivalent is not formed, but is replaced by a bivalent and a univalent, through too few chiasmata in autotriploids or non-homology in allotriploids, more irregularity in the distribution is observed. This is due to the fact that the univalent may not be included in the division spindles at the first or second meiotic divisions, and when this occurs it is generally lost in the cytoplasm. When the univalent is included in the division it will divide equationally at the first or the second division and be transmitted at random at the alternative division.

In triploids where univalents are more usual than trivalents or where the division is very irregular, gametes may be produced with chromosome numbers higher than $2x$ (e.g., *Phleum*) due to random inclusion of univalents in a cell.

The meiotic division in triploids is therefore irregular. Lagging of one or more univalents on the spindle is frequent and the *tempo* of the process is disorganised. If several univalents are lagging they may nullify the reduction division resulting in restitution nuclei as described under the "Origin of Polyploids." The cytological behaviour of pentaploids is somewhat similar to that of triploids.

One might expect from the above behaviour that a triploid would give derivatives with chromosome numbers ranging from the

diploid to the tetraploid number and with the greatest number having the $3x$ chromosome number. With the exceptional case of some *Enothera* species, however, derivatives with the $2x$ and $4x$ numbers are the most frequent, together with a few forms with chromosome numbers of the $2x + 1$, $2x + 2$, $4x - 2$, $4x - 1$, $4x + 1$, $4x + 2$ type.

Progeny of Triploids. When the cross $3x \times 2x$ is made in *Datura* the progeny consists of 53% of $2x + 1$ forms, 28% of $2x$ forms, 16% of $2x + 1 + 1$ forms and 1.4% of forms with other chromosome numbers. Similar proportions have been found in tomato (Lesley, 1928) and maize (McClintock and Hill, 1931).

Selfing a triploid *Datura* generally gives a small proportion of tetraploids together with 56% of $2x + 1$ forms. The proportion of tetraploids from selfed triploids of tomato is much higher than in *Datura*. Unfortunately, there are little data of the cross $3x \times 2x$ in *P. sinensis* or tomato.

The reason for the discrepancy between the observed chromosome numbers of triploid derivatives and those expected from cytological examination is bound up with the viability of the gametes and zygotes. This in turn depends on the genetical constitution. It is expected that the behaviour of factors in a normal haploid nucleus will be different from that in a nucleus containing reduplicated parts of the chromatin as in $x + 1$, $x + 2$, etc., gametes. The amount of reduplication of a part of the chromatin as compared with the rest of the chromatin is probably a measure of the unbalance of the genetical constitution. Under different conditions—diploid style or embryo-sac, triploid and tetraploid style, etc.—the gametes with different proportions of reduplications will react differently to the selective action (cf. Darlington, 1929 *b*, and Darlington and Moffett, 1930, etc.). This will be further considered under trisomics.

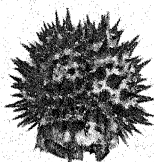
The characteristic sterility of triploids is due to the production of a large proportion of gametes containing duplications and deficiencies (see p. 125).

TRISOMICS

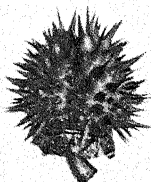
The unbalanced forms with $2x + 1$ chromosomes given in the progeny of triploids may also arise from diploids through non-



Normal



Globe



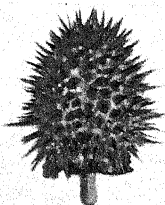
Poinsettia



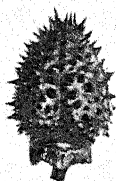
Cocklebur



Ilex



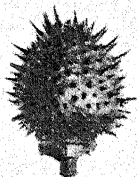
Echinus



Rolled



Reduced



Buckling



Glossy



Microcarpic



Elongate



Spinach

FIG. 34.—Capsules of the 12 primary ($2x + 1$) types of *Datura Stramonium* with a capsule of a normal plant above.
(Blakeslee, 1930.)

disjunction of one bivalent, e.g., *Matthiola incana* var. Snowflake (Frost and Mann, 1924) and *Datura*. Cold treated plants of *Datura* gave the trisomic form Poinsettia (Blakeslee and Farnham, 1923), while a whole series of forms was obtained in the progeny of a haploid *Datura* plant through irregularities in meiosis (Blakeslee, Morrison and Avery, 1927).

Primary Trisomics. Together with the normal diploid complement there is an extra chromosome of the haploid set in primary trisomics. Thus in a $2x + 1$ form of maize with $2x$ chromosomes, it was found that 9 of the chromosomes of the basic set were represented twice, but the tenth and smallest chromosome (which carries the r.g. linkage group) was represented three times.

If the haploid number of chromosomes is 12, as in *Datura* and tomato, there are twelve possible types of primary trisomics corresponding to each of the twelve chromosomes. The presence of a chromosome in excess of the normal complement is accompanied by a change, which may be observable in the expression of the characters of the individual.

Blakeslee and Belling (1924 b) and Blakeslee (1930) were able to identify all of the twelve possible trisomics by the shape of the fruit. Other parts of the plant were also affected, but fruit shape was more easily described and analysed. These trisomics have been named globe, poinsettia, cocklebur, ilex, echinus, rolled, buckling, glossy, microcarpic, elongate, reduced, and spinach respectively (see Fig. 34).

Lesley (1928) identified nine out of the possible twelve trisomics of tomato, while we understand that seven of the chromosomes of maize have been associated with known genetical linkage groups by means of the analysis of trisomics.

Trisomic Inheritance. In a plant with three homologous chromosomes *A*, *B* and *C*, random pairing followed by disjunction of two chromosomes to opposite poles and non-disjunction of the third will give the gametes *AB*, *AC*, *BC*, *A*, *B* and *C*. Therefore in a trisomic plant there will be normal disomic ratios for all factors not contained in the trivalent and a trisomic ratio for the factors borne by the trivalent.

If the trisomic plant is simplex for a factor **X** (**Xxx**), the gametic

output will be $1X : 2Xx : 2x : 1xx$ and the ratio of gametes containing the dominant and recessives will be $1 : 1$.

In a duplex trisomic (XXx) the gametic output will be $1XX : 2X : 2Xx : 1x$ and the ratio of dominant to recessive gametes will be $5 : 1$. Equal numbers of x and $x + 1$ gametes are expected to be formed on this assumption. It has been found, however, that the transmission of the $x + 1$ gametes is reduced in trisomics of maize, *Datura* and tomato, especially on the male side.

The degree of transmission of $x + 1$ gametes varies with the particular chromosome in excess. Thus the extra chromosome of the Poinsettia trisomic *Datura* is rarely transmitted through the pollen, while the Globe trisomic is transmitted in about 2% of cases. In maize and tomato the extra chromosome is rarely transmitted through the pollen.

Interesting work in this connection has been done by Buchholz and Blakeslee (1922, 1927 *a, b, c*, 1929, 1930 *a, b*). They were able to dissect the styles, and by suitable staining to observe the pollen tubes. They analysed all the possible crosses between the polyploid forms of *Datura* and also trisomic hybrids. They find, for example, that in the trisomic Cocklebur, pollen tube growth, twelve hours after pollination exhibited a bimodal curve. The two modal classes correspond to the pollen tubes carrying x and $x + 1$. The x carrying pollen grains constitute the group with greatest tube growth. The comparative rate of growth per hour was 2.6 : 1.9 mm. per hour.

The application of much pollen to the stigma reduces the proportion of $x + 1$ pollen tubes which reach the ovules. When more than 500 pollen grains from the Globe trisomic were applied to the stigma of a diploid the progeny had fewer trisomic plants. When the style was cut off after the fast-growing tubes had entered the ovary, only the x carrying pollen tubes were found to have functioned. Limited pollination followed by separation of the seeds from the lower and upper half of the ovary also showed that the $x + 1$ carrying tubes grew more slowly. In the upper half of the ovary only $2x$ seeds were found, while a higher proportion of $2x + 2$ embryos than usual were found in the lower half (*cf.* p. 20).

On the female side it is found that in place of 50%, only 30% of

the egg cells contain $x + 1$ chromosomes. McClintock and Hill point out that the univalent may or may not be included in the first and second divisions when a bivalent and univalent are formed instead of a trivalent (they have observed this fact). The univalent may undergo division either at the first or second division. If it is lost in the cytoplasm through not being included on the spindle, the number of x gametes will be increased at the expense of the $x + 1$ gametes.

In *Datura* the extra chromosome is transmitted through the female side in different proportions in the different trisomics (see Table 33). The transmission of the $x + 1$ gametes through the female is greater in *Datura*, tomato and *Matthiola* when the trisomic is pollinated with a diploid or another trisomic. Blakeslee has suggested that the greater heterosis of the embryo resulting from outcrossing is the reason for this.

TABLE 33

Transmission of the extra chromosome through the egg of primary trisomic plants of Datura and Tomato

Datura Stramonium			Tomato		
Globe . . .	29.0%		Triplo-A . .	23%	
Poinsettia . .	27.7%		„ B . .	27%	
Cocklebur . .	26.39%		„ C . .	? %	
Ilex . . .	32.0%				
Echinus . . .	30.9%				
Rolled . . .	20.1%				
Reduced . . .	18.69%				
Buckling . . .	30.9%				
Elongate . . .	10.8%				

Table 34 gives the phenotypic ratios and genetic types to be expected from a trisomic plant on the assumption that $x + 1$ pollen tubes are non-functional.

The experimental results from *Datura* and tomato agree with this theoretical expectation (see Tables 35, 36). The expected proportions of normals and trisomics cannot be given, since the transmission of $x + 1$ gametes has not yet been fully analysed.

TABLE 34

Trisomic Inheritance of an Allelomorphic Pair A, a in a (2n + 1) Mutant when the Extra Chromosome is not carried by the Pollen. Formulæ for Parents, Gametes and both 2n and (2n + 1) Offspring (Blakeslee and Farnham, 1923)

Female Parent (gametes in parenthesis).	Poli- nated by	2n offspring				(2n + 1) offspring.				
		A ₂ .	Aa.	a ₂ .	Ratio A : a	Ratio A : a.	A ₂	A ₂ a	Aa ₂	a ₃
A ₃ (A ₂ + A)	A ₃	1	1 : 0	1 : 0	1
	A ₂ a	2	1	1 : 0	1 : 0	2	1
	Aa ₂	1	2	1 : 0	1 : 0	1	2
	a ₃	1	1 : 0	1 : 0	1
	A ₂	1	1 : 0	1 : 0	1
	Aa	1	1	1 : 0	1 : 0	1	1
	a ₂	1	1 : 0	1 : 0	1
A ₂ a (2A + a + A ₂ + 2Aa)	A ₃	2	1	1 : 0	1 : 0	1	2
	A ₂ a	4	4	1	8 : 1	9 : 0	2	5	2
	Aa ₂	2	5	2	7 : 2	9 : 0	1	4	4
	a ₃	2	1	2 : 1	3 : 0	1	2
	A ₂	2	1	1 : 0	1 : 0	1	2
	Aa	2	3	1	5 : 1	6 : 0	1	3	2
	a ₂	2	1	2 : 1	3 : 0	1	2
Aa ₂ (A + 2a + 2Aa + a ₂)	A ₃	1	2	1 : 0	1 : 0	2	1
	A ₂ a	2	5	2	7 : 2	8 : 1	4	4	1
	Aa ₂	1	4	4	5 : 4	7 : 2	2	5	2
	a ₃	1	2	1 : 2	2 : 1	2	1
	A ₂	1	2	1 : 0	1 : 0	2	1
	Aa	1	3	2	4 : 2	5 : 1	2	3	1
	a ₂	1	2	1 : 2	2 : 1	2	1
a ₃ (a + a ₂)	A ₃	1	1 : 0	1 : 0	1
	A ₂ a	2	1	2 : 1	2 : 1	2	1
	Aa ₂	1	2	1 : 2	1 : 2	1	2
	a ₃	1	0 : 1	0 : 1	1
	A ₂	1	1 : 0	1 : 0	1
	Aa	1	1	1 : 1	1 : 1	1	1
	a ₂	1	0 : 1	0 : 1	1
A ₂ (A)	A ₃	1	1 : 0
	A ₂ a	2	1	1 : 0
	Aa ₂	1	2	1 : 0
	a ₃	1	1 : 0
Aa (A + a)	A ₃	1	1	1 : 0
	A ₂ a	2	3	1	5 : 1
	Aa ₂	1	3	2	4 : 2
	a ₃	1	1	1 : 1
a ₂ (a)	A ₃	1	1 : 0
	A ₂ a	2	1	2 : 1
	Aa ₂	1	2	1 : 2
	a ₃	1	0 : 1

TABLE 35

Trisomic Inheritance of the Allelomorphic Characters Purple (P) and White (p) flower colour in the Trisomic Datura Mutant Poinsettia. (After Blakeslee and Farnham, 1923)

Cross.	Number of families.	Normals.			Poinsettias		
		P	p	Dev. P.E.	P	p	Dev. P.E.
$P_3 \times P_3$	10	882	0	—	263	0	—
Calculated	—	882	0	—	263	0	—
$P_2p \times P_2p$	29	1826	220	—	692	0	—
Calculated	—	1818.7	227.3 \pm 9.58	0.8	692	0	—
$\times Pp_2$	7	292	95	—	135	0	—
Calculated	—	301	86 \pm 5.51	1.6	135	0	—
$\times p_3$	2	70	46	—	49	1	—
Calculated	—	77.3	38.7 \pm 3.42	2.1	50	0	—
$\times Pp$	4	218	36	—	121	0	—
Calculated	—	211.8	42.2 \pm 4.01	1.5	121	0	—
$\times p_2$	14	645	281	—	409	0	—
Calculated	—	617.3	308.7 \pm 9.66	2.9	409	0	—
$Pp_2 \times P_2p$	13	574	160	—	337	39	—
Calculated	—	570.9	163.1 \pm 7.59	0.4	334.2	41.8 \pm 4.11	0.7
$\times Pp_2$	35	1287	995	—	870	223	—
Calculated	—	1267.8	1014.2 \pm 16.01	1.2	850.1	242.9 \pm 9.27	2.1
$\times p_3$	4	172	292	—	142	75	—
Calculated	—	154.7	309.3 \pm 6.84	2.5	144.7	72.3 \pm 4.68	0.6
$\times Pp$	7	356	196	—	218	40	—
Calculated	—	368	184 \pm 7.46	1.6	215	43 \pm 4.04	0.7
$\times p_2$	10	219	436	—	206	84	—
Calculated	—	218.3	436.7 \pm 8.13	0.1	193.3	96.7 \pm 5.41	2.3
$p_3 \times P_2p$	2	412	233	—	185	109	—
Calculated	—	430	215 \pm 8.07	2.2	196	98 \pm 5.45	2.0
$\times Pp_2$	3	222	436	—	88	201	—
Calculated	—	219.3	438.7 \pm 8.15	0.3	96.3	192.7 \pm 5.40	1.5
$\times p_3$	1	0	143	—	0	73	—
Calculated	—	0	143	—	0	73	—
$\times Pp$	6	170	175	—	66	95	—
Calculated	—	172.5	172.5 \pm 6.27	0.4	80.5	80.5 \pm 4.28	3.4
$p_2 \times P_2p$	9	1958	1040	—	—	—	—
Calculated	—	1998.7	999.3 \pm 17.39	2.3	—	—	—
$\times Pp_2$	12	1166	2392	—	—	—	—
Calculated	—	1186	2372 \pm 18.94	1.1	—	—	—

Trisomic inheritance of doubleness in *Matthiola incana*, which, however, is complicated by lethals, is given by Frost (1931).

Secondary and Tertiary Trisomics. Early in the investigations on

Datura it was found that primary trisomics, such as Cocklebur, gave rise occasionally to other (secondary) trisomics with different morphological features, e.g., Wedge.

The genetical behaviour of primary and secondary trisomics is different, and enables one to separate the two types. The primary trisomic gives rise to forms like itself, to normals, and to a small and irregular percentage of the related secondaries. A secondary trisomic gives rise to normals, to the related primary trisomic, and to forms like itself in definite proportions. The cytology (Belling, 1927 *a*, 1928 *a*; Belling and Blakeslee, 1924 *b*) shows that in the

TABLE 36

Trisomic Inheritance of the Allelomorphic Characters Standard (D) and Dwarf (d) in the Trisomic Tomato Mutant Triplo-A.
(After Lesley, 1928)

Cross	Diploids		Trisomics	
	D	d	D	d
$Dd_2 \times Dd_2$	60	56	8	
Calculated	64.5	51.6	8.5	3
$d_2 \times Dd_2$	13	30		2.4
Calculated	14.3	28.6		

secondary trisomic there may be a closed ring of three chromosomes, while in a primary a chain only is possible. The hypothesis of these authors is that the secondary trisomic has three chromosomes, two of which are normal in structure and homologous, but the third has two similar ends, which are homologous with one end of each of the other two chromosomes (*cf.* diagram Fig. 35).

A tertiary trisomic Pinched has two Rolled chromosomes, each consisting of two segments (Sugarloaf and Polycarpic), and, in addition to the remaining eleven pairs of normal chromosomes, an extra tertiary chromosome, consisting of part of a Rolled chromosome and part of another non-homologous chromosome (Buckling). The trisome may therefore be written as (Sugarloaf-Polycarpic) (Sugarloaf-Polycarpic) and (Sugarloaf-Strawberry) (see Table 37).

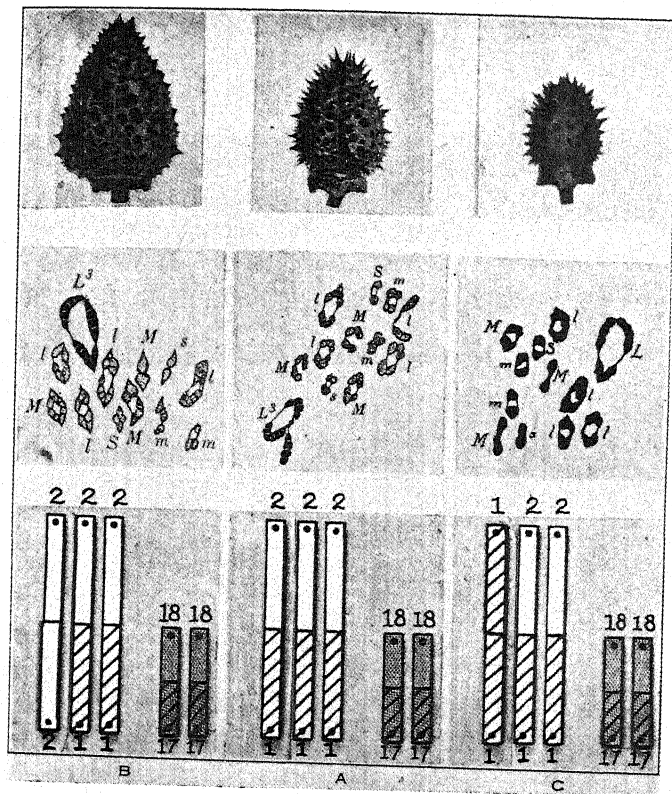


FIG. 35.—Capsule form, chromosome complement (metaphase I.) and diagrammatic explanation of the constitution of the trisome in A, the primary trisomic Rolled, B and C the related secondary trisomics Sugarloaf and Polycarpic respectively of *Datura Stramonium*. (Blakeslee, 1930.)

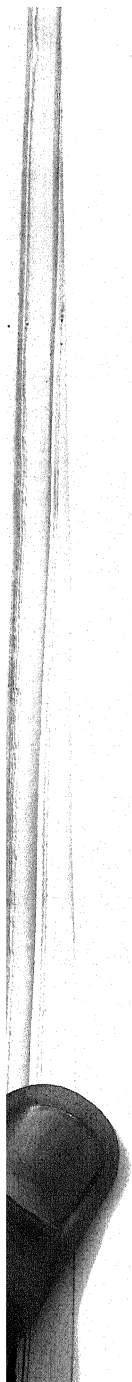


TABLE 37

List of primaries, secondaries, and tertiaries in *Datura Stramonium* arranged by size of chromosomes in the trisomic set. (Blakeslee, 1930)

[Ends of chromosomes are designated by numbers 1 to 24]

1	2	3	4	5	6
Chromosomes size class	Secondary chromosomes and (2n+2/2) type	Primary chromosomes and (2n+1) type	Secondary chromosomes and (2n+2/2) type	Tertiary chromosomes and (2n+1) type	Genes located in particular chromosome
L.....	Py (1·1).....	Rl (1·2)	Sg (2·2)	DS=2·17..... Wy=1·18. ES=2·9. Ph=2·5. Hg=1·9. trSg=12·11·2. Mp=4·6..... (3·21). (4·22).	p in Wy.
l.....	Sm (3·3).....	Gs (3·4).....			fw, Bz in 4 half. QS in Gs, half not yet determined.
l.....	St (5·5).....	Bk (5·6).....	At (6·6).....	Mp=4·6..... Ph=2·5.	
M.....	Un (7·7).....	El (7·8).....			
M°.....	Mt (9·9).....	Ec (9·10°)....	Th (10·10°)	SE=9·20°..... (10·19). ES=2·9. Hg=1·9. trSg=12·11·2..... (11·21). (12·22).	MS in either Ec or Sp.
M°.....	Wd (11·11)...	Ck (11·12°)...		X=18·13.....	in, tf, e, sky, in 12 half.
M.....	Not named (13·13)...	Mc (13·14)...	Not named (14·14).		al.
M.....	Sc (15·15)....	Rd (15·16)....			tc in 16 half.
m.....	Df (17·17)....	Pn (17·18)....		DS=2·17..... WY=1·18. X=18·13. SE=9·20°..... (10·19). trIx=(20·19·23). (3·21). (4·22). (11·21). (12·22).	c, wt in 17 half; p in 18 half.
m°.....	Dv (19·19)...	Sp (19·20°)...			sh. MS in either Sp or Ec.
S°.....		Gl (21·22°)...			sc, bb, pl.
s.....		Ix (23·24)....		trIx=(20·19·23).	sw.

The ends 10°, 12°, 20°, and 21° are characterised by terminal humps.

Rl = Rolled	Py. = Polycarpic	Sg. = Sugar loaf	DS =
Gs = Glossy	Sm. = Smooth		Wy. = Wiry
Bk = Buckling	St. = Strawberry	At. =	ES. =
El = Elongate	Un. = Undulate		Ph. = Pinched
Ec = Echinus	Mt. = Mutilated		
Ck = Cocklebur	Wd. = Wedge	Th. =	Hg. = Hedge
Mc = Microcarpic			trSg. =
Rd = Reduced	Sc. = Scalloped		Mp. = Maple
Pn = Poinsettia	Df. = Dwarf		X =
Sp =	Dv. =		trIx =
Gl = Globe			
Ix = Ilex			

Another tertiary trisomic Hedged has two Rolled chromosomes and a "tertiary" chromosome (Polycarpic-Mutilated).

On the theory of specificity of pairing a plant with a chromosome constitution, $BA\ AA\ AB$ may exhibit a ring of three chromosomes at meiosis. A secondary trisomic of *Datura* having three chromosomes of this constitution will therefore have the following gametic output (the remaining eleven chromosomes of the normal gametic complement are omitted in each case): — $1AB\ AB\ (x + 1$ primary "trisomic" gamete): $2AA\ AB\ (x + 1$ secondary "trisomic" gamete): $2AB$ (normal gamete): $1AA$ (abnormal reduplicated and deficient gamete).

Corresponding to each primary trisomic, two secondaries of the types $AB\ AB\ BB$ and $AB\ AB\ AA$ are expected. Out of the twenty-four expected secondary trisomics in *Datura* fourteen have been found by Blakeslee and his co-workers (see Fig. 35).

Tertiary trisomics result from segmental interchange between one of the trivalent chromosomes and a non-homologous chromosome. Thus, if the original chromosome was AB in a primary trisomic, inversion would produce AA and BB (secondary trisomics) and segmental interchange would produce AC , BD , etc., where C and D are segments of a chromosome not homologous with those of the trivalent.

Table 37 gives a list of the primary trisomics and corresponding secondaries and tertiaries in *Datura*. They are arranged according to the length of the chromosomes of the trisomic set and the genes located in particular parts of chromosomes are also given. The American system of numbering the twenty-four ends of the chromosomes is employed instead of the English system where letters are used.

The tertiary chromosomes, represented by figures in parentheses, are those whose ends are known, but whose morphological effect when present as extras is unknown.

BALANCE

One of the most convincing proofs of balance between factors was given by Bridges (1922) on the sex determination in *Drosophila melanogaster*. He proved that the balance between the X

chromosome and autosomes (A) is responsible for the sex determination. When the two X chromosomes in diploid flies (sex chromosomes, see p. 85) are balanced by the diploid set of autosomes, the individual is female ($2X : 2A$), and the male is obtained by the upset of this balance between the X and autosomes ($1X : 2A$). The X chromosomes contain female determiners and the autosomes (except the fourth chromosome) contain male determiners. It is well known that the Y chromosome is concerned with fertility, but not with sex determination (Stern, 1926 *a, b*, 1927 *a, b*). Alteration of this balance between X and A in plus or minus direction yielded

TABLE 38

Relation of Sex to Chromosomes in Drosophila melanogaster.
(Bridges, 1922)

Sex.	X-chromosomes.	Sets Autosomes.	Sex Index.
Super female . . .	3	2	1.5
Female { triploid . . .	3	3	1
{ diploid . . .	2	2	1
Intersex { ♀-type . . .	2	3 (- IV)	.67 +
{ ♂-type . . .	2	3	.67
Male . . .	1	2	.5
Super male . . .	1	3	.33

super female $3X : 2A$, intersex $2X : 3A$, and super male $X : 3A$ individuals (see Table 38).

The trisomics, of *Datura*, of tomato (Lesley), of *Matthiola* (Frost, 1919; Frost and Mann, 1924; Lesley and Frost, 1928), and of maize (McClintock, 1930) give many illustrations of the effects of genic balance and shed considerable light on the genetic constitution of plants and animals.

The morphological changes brought about by the reduplication of an identifiable part of the chromatin confirm the general view of the genetic differences of the parts. Each part of the chromatin content is specifically differentiated genetically.

The effect of an extra chromosome upon character expression is very similar to that of single factors, but it is obvious that a number

of factors are involved. Thus in tomato Lesley has found triplo-F with pale green foliage and triplo-E with dark green foliage, and Blakeslee has shown that Glossy and Cocklebur trisomics have respectively darker and lighter flower colours than normal. It is important to notice that neither the Glossy nor Cocklebur chromosome carries the factor P for purple flower colour. In Table 38 it will be seen that intersexual *Drosophila* flies with two fourth chromosomes present are inclined more to the female side than when all three are present. Again, the trisomics "large leaved" and "slender" in *Matthiola* are contrasting types as regards leaf shape and habit of growth (Fig. 36). Thus we see that there must be specific factors in the extra chromosome which increase or decrease the power of expression of the identified and unidentified factors in the remaining chromosomes.

A particularly informative example is shown by Sturtevant and Schultz (1931). They worked with a form of *Drosophila melanogaster* in which two X chromosomes were attached to one another or to another chromosome. Therefore the derivatives had reduplications of parts of the X chromosome. They found that scute in the presence of certain reduplicated parts of the X chromosome behaved as if dominant to normal bristle, but in the presence of other parts or in normal flies it was recessive. The authors, by this means, isolated two modifying factors on the X chromosome and have suggested several others which affect the expression of the scute allelomorph series.

In *Datura*, tomato and *Matthiola* attempts to recognise definite parts of chromosomes which affect character expression in a definite way are now being carried on. Obviously the effect of the differentiated portions of chromatin is a function of their genetical content, and it should be realised that only groups of factors and not single factors are being identified.

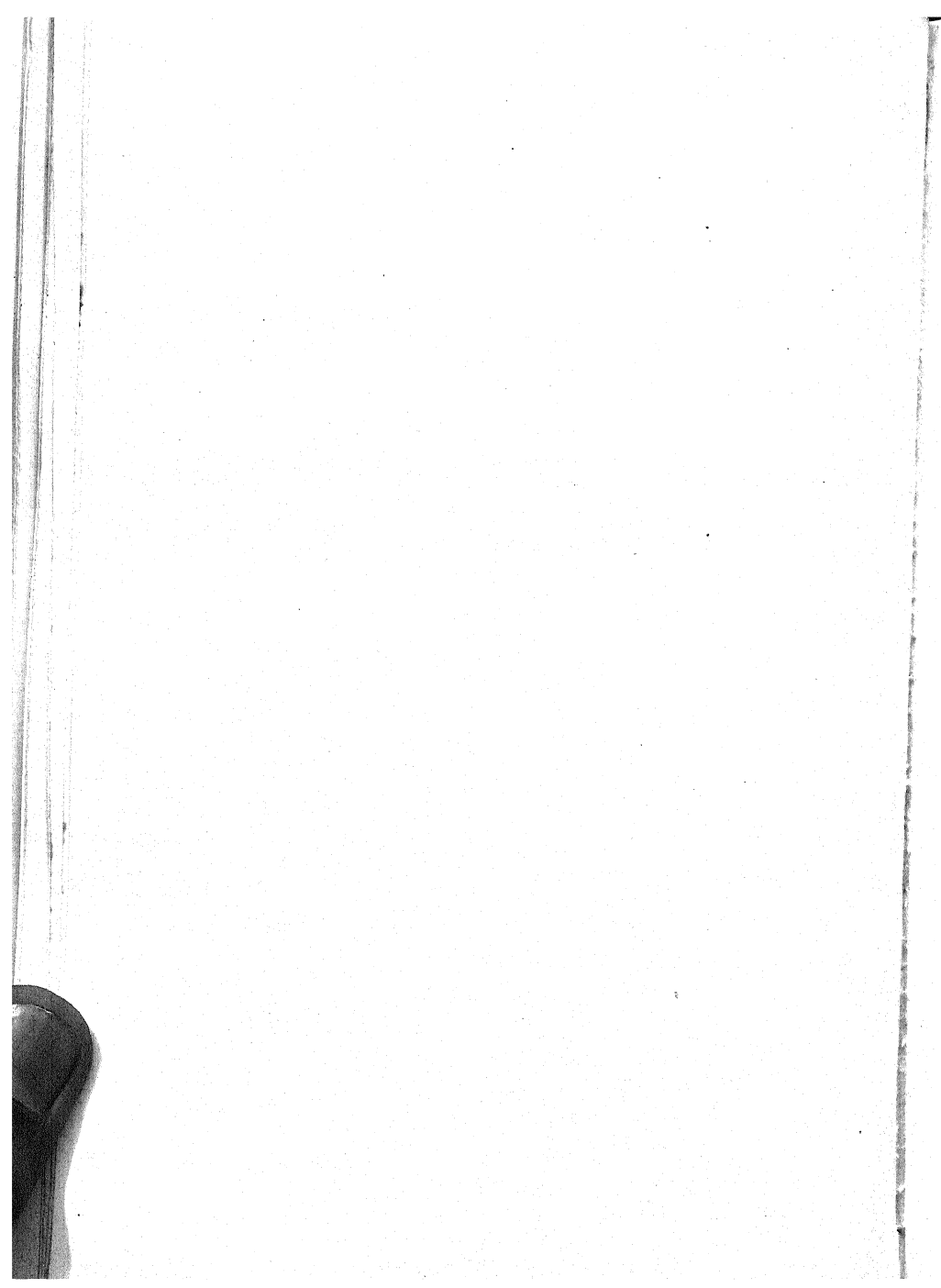
For example, it is found that the extra chromosome in the secondary trisomics of *Datura* gives a different character expression to the plant as compared with the extra chromosome in the corresponding primary trisomic. The two secondaries, Sugarloaf and Polycarpic correspond to the primary trisomic Rolled. What does this indicate?



FIG. 36.—Types of *Matthiola incana* with one, two and three extra chromosomes. From top left : Normal (14), Slender ($14 + 1$), extreme Slender ($14 + 2$); below : Large ($14 + 1$), Large Slender ($14 + 1 + 1$), Large extreme Slender ($14 + 1 + 2$). The "Slender" chromosome makes the leaves narrower; the "Large" chromosome makes the leaves fewer. (Frost, 1927.)



FIG. 37.—Normal, trisomic Small, extreme Small (tetrasomic diploid), and extreme Small (disomic haploid) plants of *Matthiola incana*. (Lesley and Frost, 1928.)



In the normal *Datura* there are four chromosome segments, two of which may be called Sugarloaf and two Polycarpic. Their balance with the remainder of the chromosome complement is such that a normal capsule shape is produced. When there are three segments of each, as in the primary trisomic, we obtain the Rolled characteristics. When there are four Sugarloaf segments and two Polycarpic together with a normal complement of other chromosomes we obtain the Sugarloaf characteristics. The balance of factors carried by the Sugarloaf segments to those carried by other segments determines the particular character expression of the plant.

The same phenomenon is seen in another trisomic Nubbin and further exemplifies the complexity and possibilities in factor balance (Blakeslee, 1927 *a, b*). Nubbin arose through X-raying the parent plant; a valuable means of creating unbalanced forms for analysis. Three of the chromosomes in terms of segments are (Sugarloaf-Polycarpic), (Mutilated-Polycarpic) and (Sugarloaf-Strawberry). Sugarloaf and Polycarpic together constitute the Rolled chromosome, therefore there is the equivalent of two Rolled chromosomes (normal balance). In addition, there are two segments, Mutilated and Strawberry, derived from two different non-homologous chromosomes, therefore the character Nubbin results from the new balance produced by the excess of one dose of Strawberry and of Mutilated above the normal complement. This might be termed unbalance.

The haplo-IVth and triplo-IVth *Drosophila melanogaster*, containing $2x - 1$ and $2x + 1$ chromosomes respectively further identify the genetical specificity of the chromosome. Characters, such as broad wings, rough eyes, pale body colour and small size of the $2x - 1$ flies are in contrast to the narrow wings, dark body and smooth eyes of the $2x + 1$ flies. Flies with a normal chromosome content occupy an intermediate position for these characters.

In the progeny of Small, a trisomic ($2x + 1$ fragment) of *Matthiola*, Lesley and Frosts (1928) found two plants with the Small character greatly intensified. They were similar to one another and resembled tetrasomic Small ($2x + 2$ fragments). One, indeed, was found to be the tetrasomic diploid, while the other was a disomic haploid

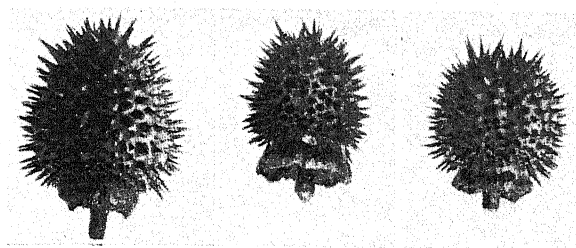
($x + 1$ fragment) (see Fig. 37). The equal balance of $2x + 2$ and $x + 1$ is reflected in the similarity of the characteristics. The Globe mutants in *Datura* $2x + 1$, $2x + 2$, $4x + 1$, $4x + 2$, $4x + 3$ exhibit a range in degree of expression of the Globe character. As expected, the $4x + 1$ is least unbalanced and the $2x + 2$ form is most extreme. (See Fig. 38).

The number of times the same factor is present in an individual does not have so great an effect as the proportionate number of times the factor is repeated in comparison with the rest of the genetical content. The haploid *Drosophila*, $X : A$, is a female like the diploid $2X : 2A$ and triploid $3X : 3A$ (Bridgés, 1925 b). Haploid, diploid, triploid and tetraploid plants are generally similar in appearance except for growth rate differences. Aneuploid forms, on the other hand, show more striking differences from diploids.

In maize McClintock remarks that the smallest chromosome carrying the r.g. linkage group has hardly any effect upon the appearance of the individual when it is present three times. The loss of a chromosome from the diploid complement is always more drastic than the addition of a chromosome, while a plant of the constitution $2x + 1 + 1$ is usually more vigorous than one of the constitution $2x + 2$. In *Datura* $2x - 1$, $3x - 1$ and $4x - 1$, forms have been obtained (Blakeslee and Belling, 1924). In polyploids the addition or loss of a chromosome does not cause so great unbalance as in diploids, e.g., wheat and oats, $6x + 1$, $6x - 1$ (see p. 229), *Datura*, $4x + 1$, $4x - 1$, *Nicotiana Tabacum*, $4x + 1$, $4x - 1$ (see p. 324), $4x + 1 - 1$, $4x + 1 + 1 - 1 - 1$ forms in *Datura* have the $4x$ number of chromosomes but are unbalanced. The degree of unbalance was considered by Darlington (1928) and Darlington and Moffett (1930).

The effect of unbalance on the viability of gametes has already been mentioned in connection with trisomic inheritance. Important work on pollen germination of the various balanced and unbalanced forms of *Datura* has been carried out by Buchholz and Blakeslee (1922, 1927 a, b, c, 1929, 1930 a, b), Blakeslee and Cartledge (1926, 1927) and Davenport (1924, 1925). For full information on this problem the reader is referred to these original papers.

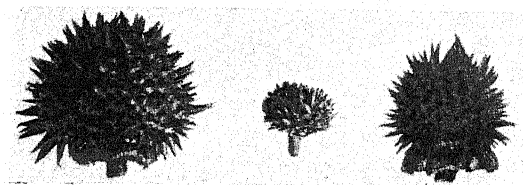
In the gamete, as in the zygote, the effect of unbalance varies for



$2x$.

$3x$.

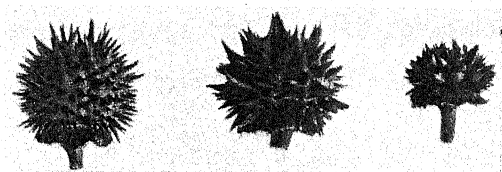
$4x$.



$2x + 1$.

$2x + 2$.

$3x + 1$.

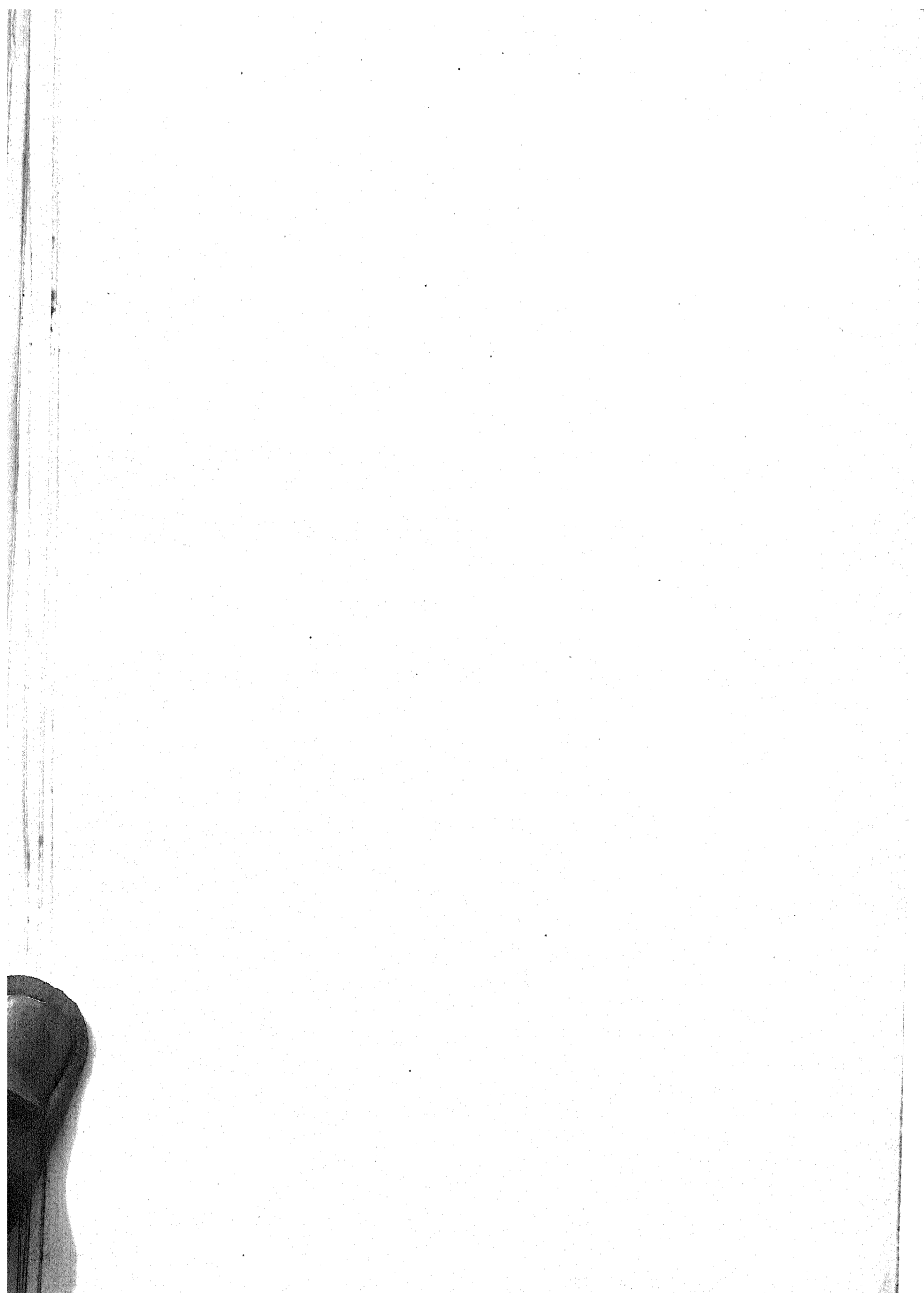


$4x + 1$.

$4x + 2$.

$4x + 3$.

FIG. 38.—Normal diploid, triploid and tetraploid capsules of *Datura Stramonium* are shown above. Below are capsules of forms having one or more extra chromosomes of the Globe set. (Blakeslee, 1930.)



different chromosomes. The extra chromosome in the pollen of trisomic Cocklebur causes the growth of the pollen tube to be slower than that of a normal pollen grain (see p. 244). The trisomic Rolled produces pollen containing an extra R1 chromosome. This pollen germinates but the growth of the tubes is slow and they swell and burst just below the stigma. When two extra chromosomes are present as in $2x + 2$ Globe, or in a $2x + 1 + 1$ plant, the unbalance in the gametes is greater and there is an increase in the amount of abortive pollen.

Chromosome deficiency seems to have the greatest effect on the gamete. Deficient pollen is always abortive. Haploid plants of *Datura* produce a large proportion of abortive pollen grains with less than the complete haploid complement. Further, the gametes which function never have less than the haploid set of chromosomes, since no $2x - 1$ forms have ever been found in the progeny.

Secondary trisomics produce a higher average of abortive pollen than their respective primaries, since they produce a higher proportion of deficient and unbalanced gametes. The following examples will demonstrate this fact and also the different effects of different degrees of unbalance, according to which part of the chromosome is causing the unbalance.

Sugarloaf (see p. 249), the secondary trisomic of Rolled, produces four types of gamete in the following proportions:—

$$2(x + \text{Sg}) : 2(x) : 1(x + \text{Rl}) : 1(x - \text{Rl} + \text{Sg}).$$

The (x) class of pollen tubes grow normally, the $(x + \text{Sg})$ class grow at two-thirds the normal rate, the $(x + \text{Rl})$ class grow slowly then burst, while the $(x - \text{Rl} + \text{Sg})$ class of pollen grains are abortive. Here the R1 chromosome in excess causes the pollen tubes to burst. The excess of 2Sg parts of the R1 chromosome only slows the growth of the tubes, whereas the deficiency of the Polycarpic part of the R1 chromosome with the excess of 1 Sg part over the normal balance causes abortion of the pollen grains.

The other secondary trisomic of Rolled, namely, Polycarpic, produces the following gametes: $2(x + \text{Py}) : 2(x) : 1(x + \text{Rl}) : 1(x - \text{Rl} + \text{Py})$. The (x) class of pollen tubes grow normally, the $(x + \text{Py})$ class of pollen grains do not germinate, the $(x + \text{Rl})$ class

of tubes burst and the $(x - Rl + Py)$ class of pollen grains are abortive. This behaviour is similar to that of Sugarloaf except that it shows the different effect of the excess of 2 Py parts of the Rl chromosome as compared with 2 Sg parts of the Rl chromosome.

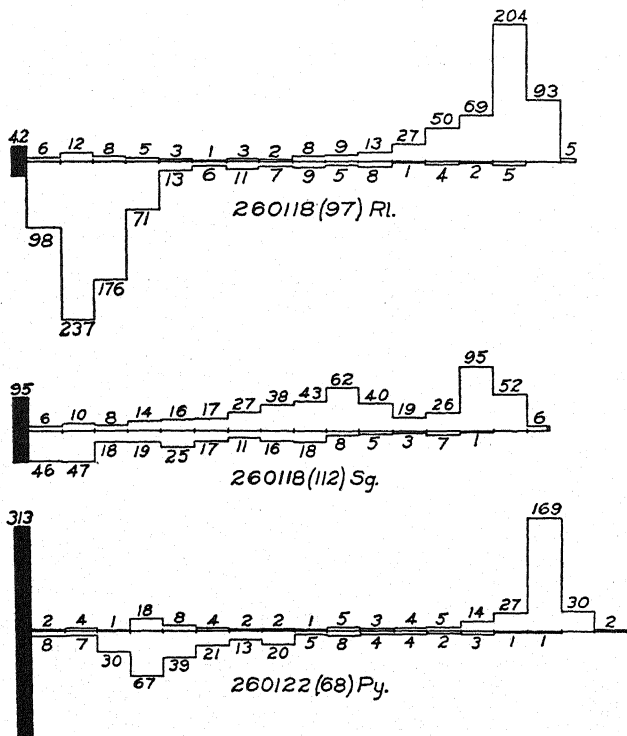


FIG. 39.—Diagrams of pollen distributions in tests of the pollen of Rolled (Rl), Sugarloaf (Sg) and Polycarpic (Py). The ends of the pollen tubes were counted and plotted; the spaces on the datum line are 2 m.m. intervals. (Buchholz and Blakeslee, 1930.)

The former prevents the pollen from germinating while the latter only slows the growth of the pollen tubes.

From histological studies Blakeslee and Buchholz (1930) constructed the above diagrams (Fig. 39), which illustrate the differences in behaviour of pollen grains and pollen tubes of different constitutions.

Triploids necessarily produce a large proportion of unbalanced gametes (see p. 240 on cytology of triploids). In triploid *Datura* there is 43% of bad pollen grains. This is mainly due to unbalance through their containing more than one extra chromosome. In tetraploids there is only 5% more bad pollen than in diploids. More irregularity in the reduction division takes place in tetraploids than in diploids, but the unbalance of a single extra chromosome in a $(2x + 1)$ gamete is less than in a $(x + 1)$ gamete.

The progeny of triploid *Datura* and tomato show the effect of gametic chromosomal unbalance. No plants with more than 27 chromosomes were obtained and the simple trisomic $(2x + 1)$ was most frequent. As theoretically expected in a binomial series (see p. 241 on $3x$ distribution), $(2x + 6)$ would be most frequent. It is therefore concluded that chromosomal unbalance has affected gametic (and zygotic) viability.

In the diploid *Raphanus-Brassica* hybrid (Karpechenko, 1927 a, b, 1928), where no pairing takes place between the 9R and 9B chromosomes, only gametes with approximately the diploid or tetraploid number were fertile. The selfed progeny consisted of tetraploids, a few with 37-38 chromosomes, and some plants with reduced development and other peculiarities had about 54 chromosomes. No triploids were found. Triploid hybrids ($18R + 9B$) selfed gave mainly diploids and a few hyperdiploids and hypotriploids. No hypodiploids, triploids or hypertriploids were obtained.

The *Oenothera* triploid *semigigas* ($3x = 21$) when crossed with diploids such as *O. Lamarckiana* or *O. velutina* gave rise to progeny with chromosome numbers ranging from 14 to 20 with the mode in the 15 chromosome class (de Vries and Boedijn, 1924 ; van Overeem, 1920).

Evidently there is not the same unbalance created by chromosome aberration in these species as in others. This, as we shall see later, is bound up with the highly complex structural hybridity of the chromosomes of this genus.

There is a large quantity of literature on the *Datura* investigations, and for further detailed information the reader is referred to the following papers: Belling (1924, 1926, 1928 a), Blakeslee (1921, 1922 a, 1924, 1927 a, b, 1928, 1929 a, b), Blakeslee and co-workers

(1924-1930), Blakeslee and Avery (1919), Blakeslee and Belling (1924 a, b), Gager, Stuart and Blakeslee (1927) and Sinnott and Blakeslee (1922).

HAPLOIDS

In nine genera of flowering plants haploid sporophytes have been discovered, namely, *Datura*, *Nicotiana*, *Triticum*, *Crepis*, *Matthiola*, *Solanum*, *Brassica*, *Oenothera* and *Oryza*. Although the leaves and floral organs often differ slightly from the female parent, in most cases the haploids appear as reduced replicas of the mother plant, being somewhat slower in growth rate and generally less vigorous (see Fig. 40). For this reason it is believed that with the exception of two cases in *Nicotiana* they have arisen from the parthenogenetic development of an egg-cell.

Jørgensen
Kallenberg ✓
Origin. The majority of haploids have resulted from the crossing of two distantly related species (see Table 39), and it is considered that the stimulus of the foreign pollen induces parthenogenesis. By pollinating *Solanum nigrum* with *S. luteum* and other species of *Solanum*, Jørgensen (1928) obtained haploids of *S. nigrum*. He observed that the pollen tubes of *S. luteum* entered the embryo-sac of *S. nigrum*, but that the nuclei did not fuse with the egg and endosperm nuclei. The male nuclei degenerated while the egg underwent division and formed the embryo.

✓ Similarly Noguchi (1928) found that when *Brassica campestris* var. *oleifera* was pollinated by *B. oleracea* var. *gemmifera* the male nuclei did not fuse with the egg or polar nuclei but that the male nucleus stimulated the egg to develop into an embryo.

The single seed which gave the haploid wheat plant was much larger than a normal *Triticum* seed, and it has been suggested that both male nuclei of the *Aegilops* pollen tube fused with the *Triticum* central fusion nucleus to produce a giant tetraploid endosperm, while the egg developed parthenogenetically. Watkins (1932) is inclined to disagree with this suggestion.

androgenis ✓
In two cases in *Nicotiana* the haploid plants had the haploid chromosome number of the male parent and also resembled the male parent. *N. glauca* ($2n = 72$) \times *N. Tabacum* ($2n = 48$) gave a plant like *Tabacum* having 24 chromosomes. Clausen and Lammerts, (1929). *N. Tabacum macrophylla* ($2n = 70-72$) \times *N. Langsdorffii*

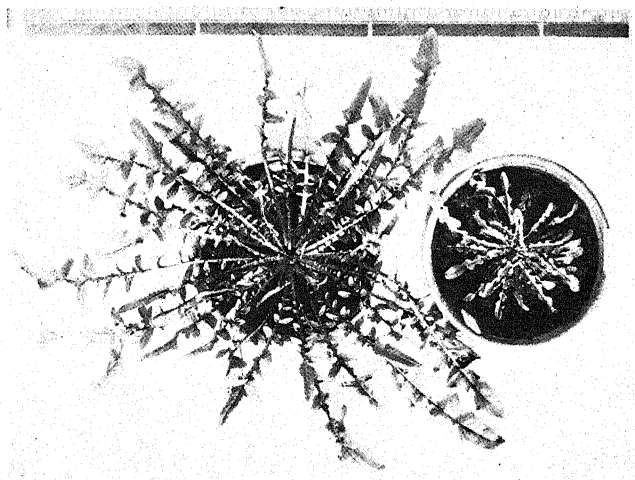


FIG. 40.—Diploid and haploid plants of *Crepis capillaris* of the same age. (Hollingshead, 1930 c.)

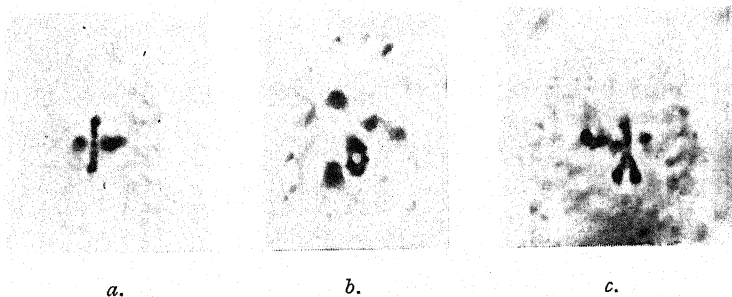


FIG. 41.—Microphotographs of metaphase I. in haploid *Enothera blandina* showing pairing of chromosomes. (Catchside, unpublished.)



($2n = 18$) gave a plant like *Langsdorffii* having 9 chromosomes Kostoff (1929). It is concluded that here the embryo developed from the male nucleus and in the egg cytoplasm (haploid merogony). Diploid merogony is not uncommon in *Nicotiana* interspecific crosses.

Low temperature has also been credited with stimulating parthenogenetic development of an egg cell. Haploid plants have been obtained by Belling and Blakeslee (1927) by pollinating *D. Stramonium* with *D. ferox*, but the first *Datura* haploid reported by Blakeslee, Belling, Farnham and Bergner (1922) arose from normal *Datura* plants which had been submitted to cold treatment about the time of self-fertilisation.

An example of the spontaneous origin of a haploid was found by Lindstrom (1929), who discovered a haploid tomato among the F_2 progeny of an intervarietal cross.

Cytology. Chromosome pairing and chiasma formation at meiosis depend on the homology of the chromosomes. In true haploids the chromosomes are all different from one another, *i.e.*, they are non-homologous and no pairing takes place. The unpaired chromosomes either segregate at random to the opposite poles and divide equationally at the second division or they may divide at the first division, when the second division will usually be suppressed, *i.e.*, non-reduction. In the *Oenothera franciscana* haploid Davis and Kulkarni (1930) found that often only one pole to the spindle was formed, the chromosomes did not split, and hence the first division was suppressed. Fusion of two or more pollen mother cells in the wheat haploid was observed to give rise to pollen grains with a high number of chromosomes. In the somatic cells of the ovary fusion of two nuclei often occurred and binucleate cells were very frequent. This is comparable with somatic doubling in *Solanum* (Jørgensen, 1928, etc.).

Solanum nigrum is a hexaploid with 72 chromosomes and in the "haploid" with 36 chromosomes Jørgensen found that from 3 to 12 bivalents were formed. This suggests that 2 of the 3 sets of chromosomes of the haploid are sufficiently alike to pair and presumably are of similar phylogenetic origin. It also provides strong evidence that *S. nigrum* is an allohexaploid.

Enothera franciscana at first metaphase in meiosis forms 5 bivalents and a ring of 4 chromosomes. Emerson (1929) finds that in the haploid 2 bivalents are frequently formed. Catcheside (unpub.) also observed pairing of chromosomes in the haploid of *O. blanda* (see Fig. 41).

Davis and Kulkarni also show 2 bivalents in their drawings, although they state that no pairing takes place. Pairing of chromosomes in haploid *Enothera* is not surprising in view of the structural hybridity of the species (see p. 287).

The consequence of irregularities in meiosis is that unreduced gametes and gametes with chromosome numbers ranging from one to the unreduced number are frequently formed. Those with less than the unreduced chromosome number (*i.e.*, with deficiencies) are inviable, due to unbalance (see p. 254). This accounts for the characteristic sterility of haploids. Only the unreduced gametes are viable, and the percentage of non-reduction varies in different haploids. In the *Matthiola* haploid, which incidentally is a disomic haploid (see p. 253) there is 70% non-reduction, whereas in *Datura* there is from 10% to 29%. Unreduced pollen grains are usually about the same size as pollen grains of a normal diploid plant.

Genetical Behaviour. Where selfed progeny of haploids can be obtained, it follows that they consist mostly of plants with the diploid chromosome number. Haploids are therefore particularly valuable for the production of diploids which are homozygous in every respect. This, of course, does not apply to haploids of structural hybrids or to some polyploids.

The selfed progeny of *Datura* haploids consist mainly of diploids, but 3.05% are trisomic ($2x + 1$) forms. The frequency of trisomic forms in the progeny of haploids is therefore much greater than in the progeny of normal diploids (0.47%), or of trisomic ($2x + 1$) parents (1.11%). Blakeslee, Morrison and Avery (1927) point out that these trisomic forms may result from non-reduction in the first division followed by non-separation in the second division or else by somatic non-separation at some stage between gamete formation and the early development of the zygote. Many of the balanced chromosomal types and primary and secondary trisomics have been derived from haploid *Datura*.

The haploid *Oenothera franciscana* on selfing gave typical diploid *franciscana* and a few other forms. A few haploids were also produced, again parthenogenetically. Back crossed with diploid *franciscana* ordinary diploid *franciscana* progeny were obtained (Davis and Kulkarni, 1930). Similar results were obtained by Stomps (1930 a). The aberrant forms he observed were like the $3x$ *semigigas* and the trisomic mutants *scintillans* and *lata*.

An interesting fact is that *O. Hookeri*, a homozygote which is closely related to *O. franciscana*, has given haploids almost identical with and in the same frequency as those from *franciscana*. The *Hookeri* haploid, however, was completely sterile.

When pollinated by a normal diploid the tomato haploid gave normal diploid progeny.

Chromosomal mutations in *Datura* are relatively common, but gene mutations are rare. Haploid *Datura* plants have produced in their immediate diploid progeny two plants, and possibly four, each heterozygous for a gene mutation. One was heterozygous for the recessive "curled" and another for the recessive "tricarpel," both these genes being located on different chromosomes. Probably each mutation arose in a single pollen grain or egg. This shows that heterozygosity is not a necessary condition before gene mutations can take place. Davis and Kulkarni also have evidence of possible gene mutation in progeny of haploid *O. franciscana*. It may be that these mutants and some of the other mutants in the progeny of haploid *O. franciscana* are the result of pairing of chromosomes which do not normally pair in the diploid. The possibility of crossing over thus provided may lead to a change in the genetical constitution of the chromosomes.

Somatic cells of the root tips of haploids commonly mutate to the diploid condition. These diploid cells are usually larger than the haploid cells. Haploid *Crepis capillaris* and *Datura* plants have also been observed to form branches of diploid and haploid tissues (periclinal chimæras) (Hollingshead, 1930 c). Pollen mother cells of haploids are also smaller than those of the corresponding diploids, being about half the volume.

TABLE 39
Origin of Haploids

	Chromosome number of haploids.	
<i>Datura Stramonium</i> ($2n=24$) cold treatment .	$x=12$	Blakeslee, Belling, Farnham and Bergner (1922).
„ „ \times <i>D. ferox</i> ($2n=24$) .	$x=12$	Belling & Blakeslee (1927).
<i>Nicotiana Tabacum</i> var. <i>purpurea</i> ($2n=48$) \times <i>N. sylvestris</i> ($2n=24$) .	$2x=24$	Clausen & Mann (1924).
„ „ var. <i>macrophylla</i> ($2n=48$) \times <i>N. sylvestris</i> .	$2x=24$	Chipman & Goodspeed (1927).
„ „ var. <i>Cuba</i> ($2n=48$) .	$2x=24$	Ruttle (1928).
„ „ var. <i>angustifolia</i> ($2n=48$) \times <i>N. glutinosa</i> ($2n=24$) .	$2x=24$	McCray (1932).
„ <i>glutinosa</i> ($2n=24$) .	$x=12$	Goodspeed & Avery (1929).
„ <i>digluta</i> ($2n=72$) \times <i>N. Tabacum</i> ($2n=48$) .	$2x=24$	Clausen & Lammerts (1929).
„ <i>Tabacum</i> var. <i>macrophylla</i> ($2n=48$) \times <i>N. Langsdorffii</i> ($2n=18$) .	$x=9$	Kostoff (1929).
<i>Triticum compactum humboldtii</i> ($2n=42$) \times <i>Egilops cylindrica</i> ($2n=28$) .	$3x=21$	Gaines & Aase (1926).
<i>Crepis capillaris</i> ($2n=6$) \times <i>C. tectorum</i> ($2n=8$) .	$x=3$	Hollingshead (1928 b, 1930 c).
„ \times <i>C. setosa</i> ($2n=6$) .	$x=3$	Lesley „ & Frost (1928).
<i>Matthiola incana</i> ($2n=14+1$ fragment) .	—	Lindstrom (1929).
<i>Solanum Lycopersicum</i> ($2n=24$) F_2 of intervarietal cross.	$x=12$	Jørgensen (1928).
<i>S. nigrum</i> ($2n=72$) \times <i>S. luteum</i> ($2n=48$) or <i>S. aethiopicum</i> ($2n=24$), etc.	$3x=36$	Noguchi (1928).
<i>Brassica campestris</i> var. <i>oleifera</i> ($2n=20$) \times <i>B. oleracea</i> var. <i>gemmifera</i> ($2n=18$) .	$x=10$	Davis & Kulkarni (1930).
<i>Oenothera franciscana</i> ($2n=14$) .	$x=7$	Emerson (1929).
„ „ \times <i>O. franciscana</i> derivatives.	$x=7$	„
„ „ \times <i>O. franciscana sulfurea</i> .	—	„
„ „ \times <i>O. longiflora</i> ($2n=14$) .	—	Stomps (1930 a).
<i>O. Hookeri</i> ($2n=14$) .	$x=7$	Davis & Kulkarni (1930).
„ „ \times <i>O. longiflora</i> .	—	Stomps (1930 a).
<i>O. rubricalyx</i> ($2n=14$) \times <i>O. eriensis</i> ($2n=14$) .	$x=7$	Gates & Goodwin (1930).
<i>O. argillicola</i> ($2n=14$) \times <i>O. biennis</i> ($2n=14$) *	—	Stomps (1930 b).
<i>O. blandina</i> ($2n=14$) \times <i>O. novæ-scotia</i> ($2n=14$) .	$x=7$	Catcheside (unpub.).
<i>Oryza</i> —intervarietal cross ($2n=24$) .	$x=12$	Morinaga & Fukushima (1931).

* Chromosome number of haploids not counted but epidermal and stomatal cells smaller than those of the diploid.

CHAPTER VIII

STRUCTURAL HYBRIDS

Genetics and Cytology—Zea—Pisum—E~~n~~othera—Gametic and Zygotic Selection—the Factor-complex Theory—Lethal Factors—Balanced Lethal Mechanism—Catenation—Segmental Interchange—Differential Segment—Origin of Half-mutants and Mass-mutants—Discussion—Genetical Linkage.

TRISOMICS are of interest in another direction. The primary, secondary and tertiary trisomics are of such a chromosome constitution that the particular chromosome in excess may form part of special associations of more than two chromosomes at meiosis. Thus in a secondary, a ring of three chromosomes can be formed

in the arrangement $\begin{array}{c} \diagup BB \diagdown \\ BA - AB \end{array}$ and in a tertiary a chain of five chromosomes is possible, viz., BA, AB, BC, CD, DC from the chromosomes AB, AB, CD, CD and BC ; the latter chromosome is the chromosome in excess and consists of parts of both AB and CD chromosomes.

Such forms were identified by Belling (1925 *a*) and Belling and Blakeslee (1926) in *Datura*. All the evidence available indicates that chromosomes pair because their parts are homologous, and that no pairing takes place between non-homologous parts. Homology is a function of the relationship of the parts of the chromosome in terms of chromomeres (cytological) or genes (genetical) according to the attitude, cytological or genetical, with which one approaches the subject. If this theory of specificity of pairing (Darlington) is adopted, one may interpret many cytological phenomena by the pairing behaviour of chromosome parts. For example, when it is found that more than two chromosomes enter into one association in a diploid, one has either to assume that non-homologous parts do pair or rearrangement of the chromatin material has taken place. The first assumption is in direct contradiction to the chromosome theory involving as it does the individuality of

the chromosome and the mechanism of genetical segregation. The adoption of the view that the chromatin material has been interchanged between chromosomes does not contradict the chromosome theory and permits a rational interpretation of a wide range of facts.

The interchange of segments between two non-homologous chromosomes can therefore be inferred from the cytological analysis of meiosis in certain diploid and tetraploid forms. The occurrence of an association of more than two chromosomes in a normal diploid, or of more than four chromosomes in a tetraploid, implies that segmental interchange has previously taken place between non-homologous chromosomes.

By means of cytological observation the following plant species have been shown to have races with interchanged chromosome segments :—

Enothera (see later for references) ; *Datura* (Belling, 1925 a ; Blakeslee, 1928, etc.) ; *Zea Mays* (Brink, 1929 b ; Burnham, 1930 ; McClintock, 1930 ; Cooper and Brink, 1931, etc.) ; *Pisum sativum* (Håkansson, 1929 a, b, 1930 a, 1931, 1932 ; Richardson, 1929) ; *Campanula persicifolia* (Gairdner and Darlington, 1930, 1932) ; *Godetia* * (Håkansson, 1925) ; *Briza media*, *Anthoxanthemum odoratum* (Kattermann, 1930) ; *Rhæo discolor*, *Zebrina pendula* and various *Tradescantiæ* (Darlington, 1929 c) ; *Matthiola incana* (Philp and Huskins, 1931).

The manner in which segmental interchange occurs is not definitely known. The stage of occurrence of segmental interchange between non-homologous chromosomes is probably the same as that between homologous chromosomes—namely, at pachytene. It is known that interlocking of chiasmata occurs in some species with structural-hybrid forms, such as *Enothera* (Catcheside, 1931 ; Darlington, 1931 b) and *Campanula persicifolia* (Gairdner and Darlington). The ring bivalents and rings involving more than two chromosomes may become accidentally entwined at the early prophase stages and remain together until anaphase. This close approximation of non-homologous chromosomes at the time of crossing over may lead to segmental interchange between non-homologous

* The case in *Godetia* is a species hybrid.

chromosomes. Darlington (1931 *c*) has suggested that interstitial translocation followed by crossing over would lead to segmental interchange between non-homologous chromosomes. Evidence will be discussed later (p. 289) which throws definite light on segmental interchange in structural hybrids.

McClintock (1930) and Cooper and Brink (1931) have furnished direct cytological evidence of segmental interchange in maize. By suitable crosses to primary trisomics, McClintock proved that the second and third smallest chromosome pairs of maize were involved in a ring of four in hybrids involving "semi-sterile 2." This ring of four chromosomes appears when a race (semi-sterile 2) is crossed to a normal race of maize.* In the prophase of normal maize plants there is a pair of small chromosomes with a knob-like structure at one end. In the ring of four chromosomes there are two chromosomes with knobs and two without knobs. One of the knobbed chromosomes is much longer than the other. As expected, if segmental interchange had occurred, the position of the attachment constriction is, in relation to the knob, identical in both chromosomes. Measurement shows that the knobless chromosomes also differ from one another in length.

If the chromosomes of the normal race are $AB\ CD\ AB\ CD$ in terms of segments and the segment B is shorter than the segment C , an interchange between them will give a chromosome AC longer than the original AB , and a chromosome BD shorter than the original CD . Pairing of similar parts will obviously result in a ring of four in the semi-sterile line 2 of the constitution $\overline{BA-AC-CD-DB}$.

Cooper and Brink examined the prophases of another semi-sterile line (5) where a chromosome with trabants is involved. The relative sizes of the segments of each chromosome (AB, BD, DC, CA) are shown in the diagram (Fig. 42), together with their method of pairing at zygotene.

It will be noticed that each of the four chromosomes can be

* It is unfortunate that the workers on maize have not clearly differentiated by their terminology the structural hybrid (*e.g.*, semi-steriles 2-5) from the parental and derivative interchanged lines which are fertile. This difficulty probably arose through the manner in which the semi-sterile was first isolated—as a structural hybrid.

distinguished, thus supporting the view that a segmental interchange has taken place in a previous generation.

Obviously, disjunction at anaphase of such a ring of four chromosomes will be distinct in type from that of a pair of chromosomes homologous throughout their length. It will be conditioned by the formation and behaviour of chiasmata following pairing of one chromosome with two others in different parts of its length and by the position of the attachment constrictions in the four chromosomes.

From observations on eleven plants of *Pisum*, Håkansson has found that 304 rings of four chromosomes disjoined in such a way that alternate chromosomes passed to the same pole, and that in 306 rings adjacent chromosomes passed to the same pole. The ring may be represented as $AB\ BD\ DC\ CA$.

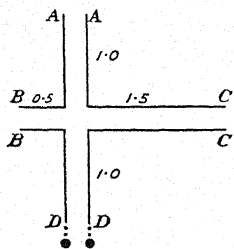


FIG. 42.—See text.
(Cooper and Brink, 1931.)

Paternal and maternal derived chromosomes alternate in the ring. The first method of separation with alternate chromosomes passing to the same pole gives rise to two types of gametes containing the complements AB , CD and DB , AC , *i.e.*, similar to those which formed the structural hybrid. When

adjacent chromosomes pass to the same pole (*i.e.*, non-disjunction) duplication and deficiency of the genetical material results. The gametes resulting from this latter method of separation will therefore be unbalanced and probably abortive.

Consequently, as expected, a ring-forming structural hybrid with 50% of non-disjunction in the ring, produces 50% abortive pollen and ovules. It is possibly significant that abortion in ring-forming hybrids has generally been found in those plants where ovule abortion is easily recognised by inspection of the fruit, and has rarely been noticed in those species with syncarpous fruits.

Hammarlund and Håkansson (1930), Richardson (1929), and Pellew and Richardson Sansome (1931) found 50% sterility associated with ring formation in *Pisum sativum*. E. R. Sansome (1932) found two lines with 50% sterility associated with a ring of four chromosomes. She also found that the semi-sterile line of

Håkansson was distinct from one of these lines. Burnham (1930), McClintock (1930), Cooper and Brink (1931), have also reported five separate lines of maize showing rings of four chromosomes and 50% sterility.

Lines of *Datura* have been found which gave 50% pollen abortion on crossing to a standard line (1a) whereas when crossed to another line (7) which gave 50% abortion of pollen with (1a), no pollen abortion was observed. These hybrids had no configurations of four chromosomes, but in F_1 hybrids between (1a) and "B whites" closed rings of four chromosomes were frequent and were accompanied by little or no sterility (Blakeslee, 1928, 1929a). See

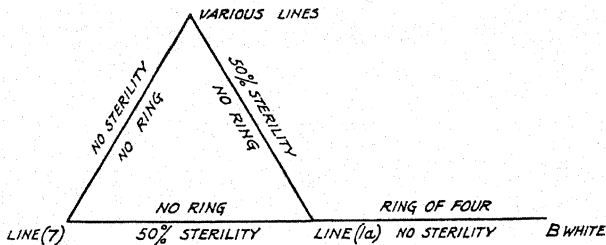


FIG. 43.—Diagram of sterility and ring formation in *Datura* hybrids.

Fig. 43. On the other hand, Blakeslee and Cartledge (1927) have found that tertiary trisomics of *Datura* when crossed to other lines showed both sterility and multiple association of chromosomes.

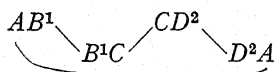
As pointed out by Pellew and Sansome (1931), gametic abortion without ring formation can be explained on the segmental interchange hypothesis. If the interchange has involved only a small part of the chromosomes the frequency of chiasmata in the interchanged parts will be small. Hence rings of four chromosomes will be rarer than bivalents. The disjunction of the bivalents $AB.AC$ and $BD.CD$ will be independent; in 50% of the resulting gametes duplicated and deficient genetical material will be present. On the other hand, if a ring of four chromosomes is controlled in disjunction in such a way that the parental complements are recovered in a large proportion of cases, there will be little sterility.

It is obvious that if the segments of two non-homologous chromo-

somes are interchanged the linkage between factors on those segments and those on the remaining segments of the chromosomes participating in the interchange will be influenced in a definite manner.

There are three possibilities :—

(1) Two allelomorphic pairs of factors are situated on different pairs of chromosomes in both normal and interchanged lines. The chromosomes of the normal line are $AB^1 CD^2$, where the indices represent the loci of the factors. The interchanged line is $B^1C D^2A$. The factors in both lines will show independent segregation. In the hybrid between the lines a ring



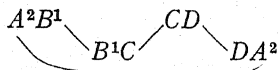
will be formed. The viable gametic types will be the same as the gametic complements of the parents. Hence the factors on the *B* and *D* segments might not segregate independently, but might appear linked. The inviable gametes will contain the segment recombinations, while the viable gametes will only contain the segment arrangements as in the parents.

Hence apparent linkage between factors on different chromosomes will be caused by "chromosomal linkage" or catenation (Gates, 1931). Crossing over between the locus of the factor and the point of interchange will occur and give rise to recombination between the factors considered. Hence the cross-over value between the two factors is the sum of the distances between them and the point of interchange.

(2) Two pairs of factors are located on different segments of one pair of chromosomes in the normal line and are separated in the interchanged line. $A^2B^1 CD$ is the normal line, the indices indicating the loci of the two factors. The interchanged line is B^1C and DA^2 . In the normal line the factors will show linkage

with one another (if less than 50 units apart), but in the interchanged line they will be independent.

In the hybrid between the two lines the chromosomes will form a ring



The only viable gametes will be those similar to the parental complements (A^2B^1CD and B^1CDA^2). Hence the hybrid will show linkage between the factors due to the combination of genetic linkage and catenation.

(3) Two pairs of factors are located on different segments of one pair of chromosomes in the interchanged line and are separate in the normal. This is the reciprocal of (2).

In all three possibilities it will be seen that the point of interchange is a critical point for the control of the linkage value between the factors. The linkage map of such a ring of four chromosomes is in the form of a cross with the length of the arms proportional to the length of the segments and with the centre of the cross at the point of interchange, when it coincides with the attachment constrictions (Fig. 44).

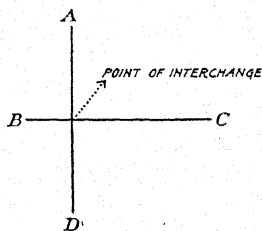


FIG. 44.—Diagrammatic representation of the linkage map of a ring of four chromosomes.

Some genetical investigation has been made on ring-forming hybrids in maize and peas, but much more requires to be done.

Hammarlund (1928) was the first to report an experiment on such a race of *Pisum sativum*. **A** was a factor for flower colour and **Gp** for green pod. These were independent in the normal races of *Pisum*, but were found to be linked in the hybrid between the normal and the interchanged line. The cross was made thus: **A Gp**, interchanged line \times **a gp**, normal line. Results of the F_2 and backcross to normal line **a gp** are available, but from them it is not possible to say whether the linkage observed is due to genetic linkage or to catenation. We must know

whether or not the parental lines, or those derivative lines of the F_1 , which correspond to the parental lines, show independence between the factors. If one of the parental lines showed linkage between the factors we would have a state corresponding to the possibilities (3) or (2) above. If there were no linkage it would correspond to possibility (1). Pellew and Sansome found in hybrids between a Tibetan variety and a commercial strain that those plants heterozygous for the allelomorphs round (R) and wrinkled (r), had a ring of four chromosomes and 50% gametic abortion, while the plants homozygous for round and wrinkled had no ring and no sterility. Analysis of the families showed that a small proportion of the homozygotes had rings and sterility and a small proportion of the heterozygotes (Rr) had no rings.

If we suppose that the factors Rr are located in the ring of chromosomes and that crossing over takes place between the locus of R and the point of interchange, then an interchanged line with the factors RR and a normal line with the factors rr will be formed. These on hybridisation with the original lines will reverse the correlation between ring formation and heterozygosity of Rr .

In maize Brink (1929 b), McClintock (1930), McClintock and Hill (1930), Creighton and McClintock (1931), and Rhoades (1931), have identified the linkage groups which were involved in the rings in the lines semi-sterile 1, 2 and 4.

The chromosomes in the ring of semi-sterile 2 contained the linkage group $C - wx$. The chromosomes in the ring of semi-sterile 1 contained the linkage groups $P - br$ and $b - lg$ and semi-sterile 4 had $b - lg$ and $pr - v2$ linkage groups in the ring. The points of interchange in the rings of semi-sterile 2 and 4 were known in relation to the loci of the factors of these linkage groups. In the case of semi-sterile 2 the position of the factors $C sh$ and Wx were known in relation to the point of interchange and also to the knob-like structure which was mentioned earlier.

It will be remembered that the interchanged chromosomes bearing the knob-like structure are different in length from the knobbed chromosome in the normal races; therefore they can be cytologically identified. There are normal races which do not have

the knob-like structure on the homologous chromosome. Creighton and McClintock crossed a plant, semi-sterile and heterozygous for the interchange chromosome (knobbed interchange — knobless normal) with a normal plant homozygous for knobless) and obtained the following chromosome types in the progeny:—52 knobless normal — knobless normal, 47 knobbed interchange — knobless normal, 37 knobbed normal — knobless normal, and 28 knobless interchange — knobless normal.

The first two categories are similar to the types of the normal and semi-sterile parents respectively, while the last two types are different and constitute the results of crossing over between the point of interchange and the knob. These figures give the cross-over percentage between the knob and the point of interchange as 39%.

The factor C and the knob are closely linked while Burnham (unpub.) *ex. McClintock* (1931) gives the cross-over percentages between the point of interchange and C sh and Wx as 33%, 32% and 13% respectively.

We have thus a useful method of identifying the position of the factors on the chromosomes in relation to definite visible points.

Similarly, Rhoades (1931) has found that the cross-over percentages between the point of interchange and several factors in semi-sterile 4 were:—

b — 1g linkage group	pr — v ₂ linkage group
ts ₁ — interchange 4%	pr — interchange 18.3%
b — „ 22.1%	v ₂ — „ 46.3%
1g — „ 47.3%	

This shows that the point of interchange lies close to ts₁ in the b — 1g chromosome, while in the pr — v₂ chromosome more factors are required to locate the exact position of the point of interchange in relation to the factor loci.

Rings of Six Chromosomes. In *Pisum sativum* (E. R. Sansome, 1932), in *Zea Mays*, McClintock (1930), Cooper and Brink (1931), in *Campanula persicifolia* and in *Oenothera*, Gairdner and Darlington (1932) plants have been produced with rings of six chromosomes by hybridisation of two plants with rings of four.

In maize, semi-sterile 1 contains the b — 1g and P — br linkage

groups in the ring of four, while semi-sterile 4 contains $b - 1g$ and $pr - v_2$. The chromosome carrying $b - 1g$ is common to both. In terms of homologous segments these two lines may be represented as $AB\ BC\ CD\ DA\ EF\ EF$ and $AB\ AB\ CD\ DE\ EF\ FC$ where segments C and D carry the $b - 1g$ linkage group. Fig. 45 illustrates the possible constitutions of the progeny:—

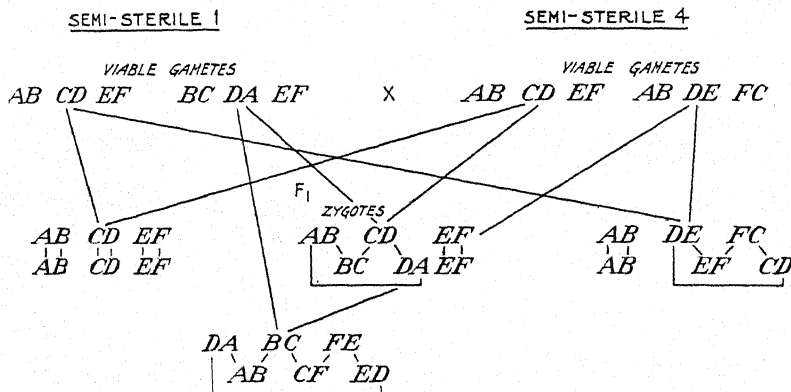


FIG. 45.—Constitutions of the possible viable gametes and zygotes resulting from a cross between two lines with different rings of four chromosomes.

We expect therefore a ratio of two plants similar to the semi-sterile parents: one plant with the normal complement of chromosomes: one plant with a ring of six chromosomes. This latter type was identified by the fact that the sterility of the plant was slightly less than 75% instead of 50%. Similarly Burnham (1930) finds that a plant with a ring of six chromosomes is formed in the progeny of the cross semi-sterile 5 \times semi-sterile 1. This indicates that semi-sterile 5 contains either the $P - br$ or $b - 1g$ linkage group in the ring of four. On the other hand, when semi-sterile 2 is crossed with semi-sterile 1, plants with two rings of four and a sterility of slightly over 75% are obtained. Hence semi-steriles 1 and 2 do not have a linkage group in common in their rings.

Gairdner and Darlington have shown that four strains of *Campanula persicifolia* from different sources were normal in segment structure while three contained rings of four chromosomes.

Two of these strains, Gm1 and Gm2, had a chromosome in common in the rings since the hybrid between them had a ring of six. Gm1 \times FdN (another structural hybrid) gave plants with two rings of four, therefore FdN and Gm1 had different chromosomes in the rings.

The importance of this work on ring-forming plants (structural hybrids) lies in the fact that they enable us to study more intensively the behaviour of parts of chromosomes which may be genetically and cytologically identified. On the genetical side the localisation of factors in terms of cytological points on the chromosomes, and the correspondence between the segregation of factors and chromosome behaviour is important. A possible explanation is provided for such a case as *Pisum sativum*, in which (1) the number of linkage groups does not correspond to the number of haploid chromosomes, and (2) different workers report different linear arrangements of linked factors.

ŒNOTHERA

Introduction. In 1886 de Vries (see de Vries, 1901) began an investigation of a population of *Œnothera Lamarckiana* which he discovered near Hilversum, in Holland. Since that time he has continued the investigations, while many other workers have been attracted to the work through the complex and novel problems which are encountered. It was found that some *Œnothera* species were not stable but on occasion gave rise to mutants, which might or might not remain stable. For example, de Vries found that *O. Lamarckiana* during eight generations of culture, gave rise to several new types, some of which had a moderately high frequency of recurrence (Table 40). Thus 53,509 offspring in one culture were true *Lamarckiana*, while 350 were of the form called *oblonga*, 229 were *lata*, 158 were *nanella*, while other forms appeared in smaller numbers. Two important differences in behaviour from that of factor segregation should be noticed. First, it is found that the mutation rate is low (total about 1.5%) and is not amenable to interpretation on a basis of normal segregation; secondly, that the new forms differ from *Lamarckiana* by a complex of characters and thereby may again mutate to plants with characteristics quite definitely different from those of *Lamarckiana*.

It is not within the province of this book to review the whole literature of the subject, but rather to indicate the directions in which the investigations now in progress are proceeding.

The earlier workers were not aware of the methods now available for investigating such a problem as that of *Oenothera*, while the complicated results which were obtained during the breeding work were inexplicable.

It was thought by some that the behaviour of *Oenothera* was distinct from that of other more fully investigated species. The

TABLE 40

Pedigree of a Family of O. Lamarckiana, 1886-99 (Data of de Vries)

Generation.	Gigas.	Albida.	Oblonga.	Rubri-nervis.	Lamarckiana.	Nanella.	Lata.	Scintillans.
I					9			
II					15,000	5	5	
III				I	10,000	3	3	
IV	I	15	176	8	14,000	60	73	I
V		25	135	20	8,000	49	142	6
VI		11	29	3	1,800	9	5	I
VII			9		3,000	11		
VIII		5	I		1,700	21	I	
Total	I	56	350	32	53,509	158	229	8

advent of cytological work on the species, however, facilitated the investigations, and since 1928 more and more workers have adopted the view that the behaviour of *Oenothera* is similar to, but much more complex than that of the ring forming diploid species already enumerated.

The genetic behaviour of species of *Oenothera*, which was studied first by de Vries and later by many other workers, appeared, until recently, to be anomalous in the plant and animal kingdoms. De Vries found that inbred *Oenothera Lamarckiana* produced in about 2% of cases several forms which were distinct in type. These sparse segregates he named *mutations* (a formerly generalised term), and supposed that they arose through some change in the immediately preceding cell generations.

Hybridisation between species was found to be comparatively easy and productive of peculiar and complicated results. Although several of the species bred true when selfed, crossing two species often gave rise to two or more distinct types of plants, and reciprocal crosses sometimes produced different results. For example, the cross, *O. Lamarckiana* \times *O. Hookeri*, produces two forms, *læta* and *velutina* (de Vries, 1913). *Læta* is similar in reciprocal crosses but *velutina* is variegated if *Lamarckiana* is the female parent. *Læta* and *velutina* do not differ solely in one character but can be separated by a group of characters. The workers (see Renner, 1914, 1917, and Honing, 1911) concluded that the twin hybrids produced in such a cross resulted from the fact that one parent (*Lamarckiana*) produced two types of gamete as in a heterozygote. Renner called the two complexes which were found in the gametes of *O. Lamarckiana*, *gaudens* and *velans* respectively. When a *velans* gamete unites with the gamete of *Hookeri*, *velutina* results, while the union of gametes bearing *gaudens* and *Hookeri* gives rise to *læta*. It is found that *O. Lamarckiana*, *biennis*, *muricata*, *suaveolens* and other similar species breed true when selfed, with the exception of a few mutations; yet they are heterozygous for two complexes. The reason why they breed true when selfed is furnished by the discovery of various anomalies in the physiology of the gametes and zygotes.

Seed Production. Seed production in selfed *O. Lamarckiana* is half that of *Lamarckiana* crossed with any other species of *Ænothera*, except *biennis* and some of its derivatives. Renner (1914) and Hiorth (1926) describe three types of fertilised ovules in selfed *O. Lamarckiana*. One half have normal embryos and endosperm and give rise again to *O. Lamarckiana*; they result from the fusion of gametes bearing the *velans* and *gaudens* complexes respectively. (It is useful to indicate the nature of the species in terms of complexes, thus—*velans-gaudens*.) One quarter of the ovules have small embryos and an empty endosperm sheath and consist of the *velans-velans* complexes, while another quarter have no embryo or endosperm: *gaudens-gaudens*. Hence it was realised that *O. Lamarckiana* bred true although heterozygous owing to the death, in the young stage, of the homozygote combinations. Meanwhile,

Heribert-Nilsson (1912) found that a red-nerved race of *O. Lamarckiana* when selfed segregated in the ratio two red-nerved to one white-nerved (566Rr : 288rr) and pointed out that the RR zygotes were eliminated. De Vries was the first to suggest that homozygotic elimination was bound up with lethal factors in *Oenothera*.

Table 41 from Renner (1917) shows the seed production of various species of *Oenothera*. From it one sees that some species,

TABLE 41
Viable Seed Production of Oenothera Species

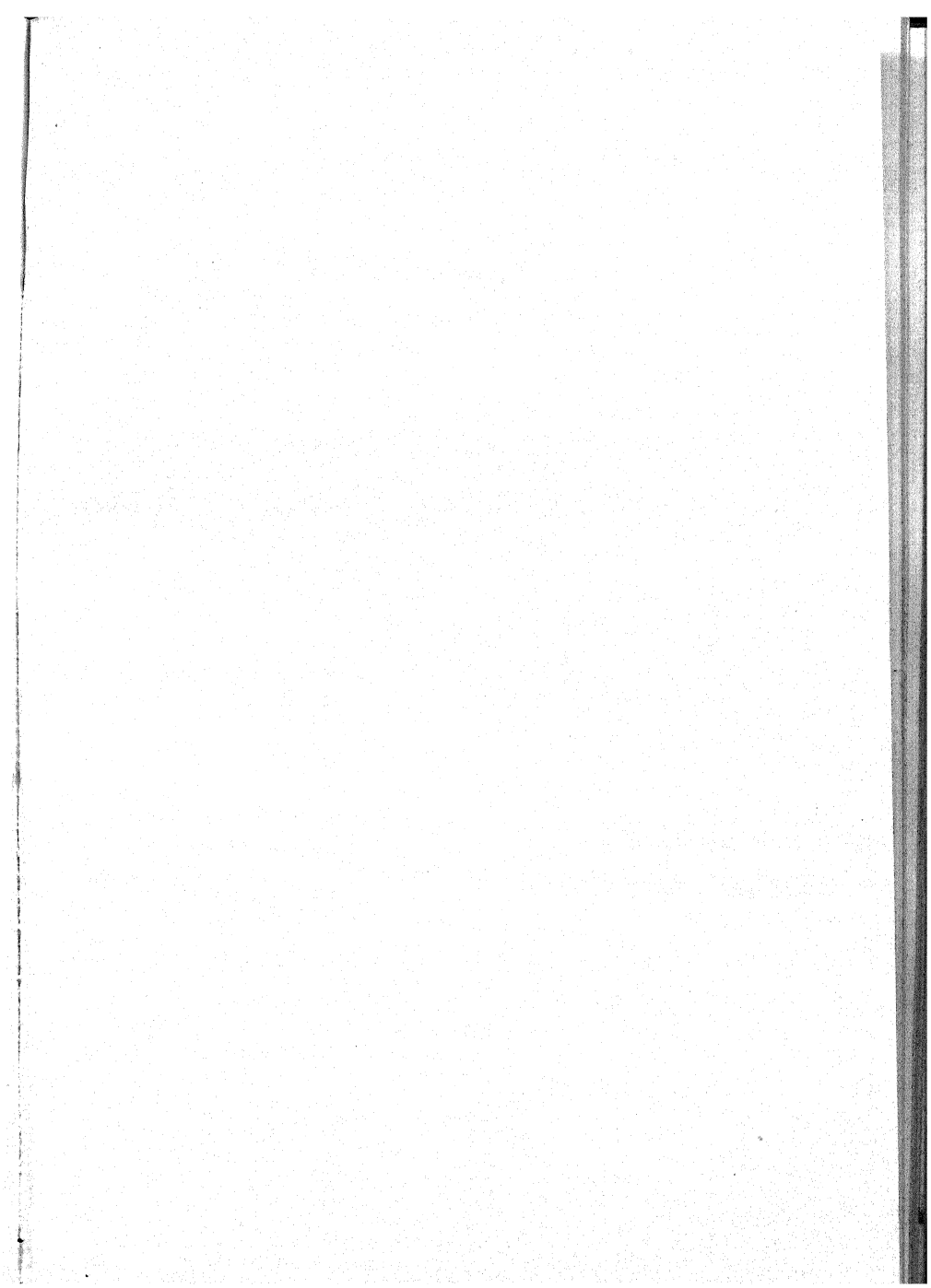
(After Renner, 1917)

100% represents a full viable seed production

	Renner's observations.	de Vries' observations.
<i>Lamarckiana</i> , Her. Nilsson —Red-nerved . . .	23-33%	—
„ „ „ —White-nerved . . .	30-49%	—
„ „ „ × <i>biennis</i> . . .	46-55%	—
„ „ „ × <i>muricata</i> . . .	91-98%	—
<i>muricata</i>	63-87%	91-97%
„ × <i>biennis</i>	0%	95%
„ × <i>Lamarckiana</i>	48-80%	96%
<i>suaveolens</i>	15-46%	12-39%
„ × <i>biennis</i>	73-88%	93%
„ × <i>Lamarckiana</i>	91-93%	89-90%

which are known to produce twin hybrids on out-crossing, have a full seed production even when selfed. *O. muricata* is such a form. Elimination of gametes, instead of elimination of zygotes, takes place in this case, but both zygotic and gametic elimination may be found in one species. Whereas *O. Hookeri* has 100% good pollen and ovules, other species have a greater or less mortality of pollen or ovules (Davis, 1910; Gates, 1915; Geerts, 1909; Renner, 1914, 1917).

Differential Lethality of Gametes. By various species crosses *O. muricata* was proved to produce two types of pollen



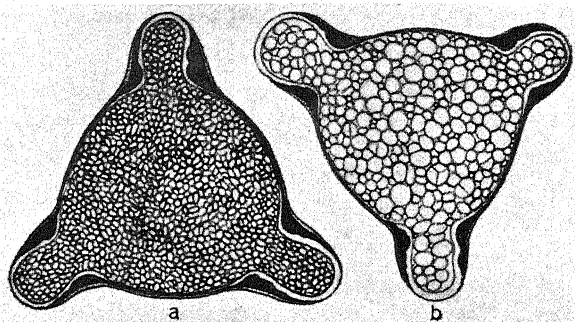


FIG. 46.—Pollen grains of *Enothera muricata*. *a*, active *curvans*, *b*, inactive *rigens*. (Renner, 1919.)



FIG. 53.—Ears of : *a*, round-glumed *turgidum* = 28 chromosome kk. Extracted type. *b*, keeled *turgidum*, parent variety = 28 chromosome KK. *c*, round *vulgare*, parent variety = 42 chromosome kk. *d*, keeled *vulgare*, the type speltoid = 42 chromosome KK. Extracted type. (Watkins, 1927.)

(called *rigens* and *curvans*). Renner (1919 b) identified the active *curvans* pollen as those grains carrying the smaller blunt-ended starch grains, as contrasted with the *rigens*-carrying pollen grains which have much longer spindle-shaped starch grains, and are non-functional or, as they are called, inactive. 50% pollen abortion can be observed in the pollen of *muricata* (see Fig. 46). Similarly, crossing experiments, using *muricata* as the female parent, show that only one type of ovule is functional, and that this type is different in genetic properties from the functional type of pollen. The active complex in the ovule is *rigens*, while the *curvans* complex inhibits embryo-sac formation. It should be noted for later remarks that in one and the same *muricata* plant, selection has been able to affect, independently and distinctly, the lethals governing egg and pollen viability. Renner (1921) found that in *O. muricata* any one of the four megaspores could give rise to the embryo-sac while in *O. Hookeri* and *O. Lamarckiana* it was mainly the one at the micropylar end of the row of four megaspores which functioned. This so-called *Renner effect*, which has also been reported in *O. nutans* and *O. pycnocarpa* (Atkinson, 1916, 1917 and Ishikawa, 1918) would account for the fact that only *rigens* megaspores function on the female side of *O. muricata*. Four megaspores result from the two divisions of meiosis, therefore *rigens* will separate to the two megaspores at the chalazal end, and *curvans* to those at the micropylar end or *vice-versa*.

Observation shows that in *O. muricata* the embryo-sac may be formed in the normal position (the micropylar end) or at the chalazal end. It is found that in both cases the embryo-sac contains the *rigens* complex. The interpretation of this is that, when the *curvans* complex is carried by the micropylar megaspore the *rigens* megaspore at the chalazal end competes with it. Since *curvans* contains lethals only functional in embryo-sac formation, the megaspore at the chalazal end containing the *rigens* complex forms the embryo sac. This is confirmed by the figures in which it can be seen that (1) when only the megaspore at the micropylar end forms an embryo-sac no other megaspore develops further, (2) when megaspores at the chalazal end form embryo-sacs the megaspore at the micropylar end is swollen but not functional. *O. muricata* therefore

has differential gametic elimination and when selfed produces a full seed production of *rigens-curvans* zygotes (Fig. 47).

An interesting example of gametic elimination is seen in the cross *suaveolens* \times *muricata*, where one of the hybrid types results from the union of the *curvans* complex from *muricata*, with *flavens* from *suaveolens*. In this hybrid two pairs of factors, **B** for large leaf *vs.* **b** for small leaf, and **M** for margined leaf *vs.* **m** for not margined leaf are arranged **Bm** *flavens*, **bM** *curvans*. The hybrid (*flavicurva*)

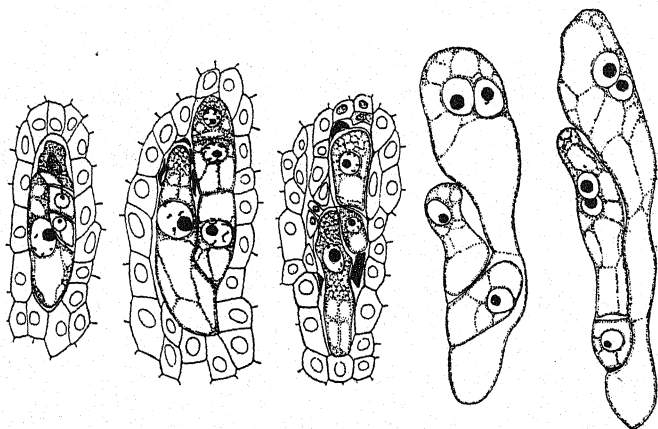


FIG. 47.—Embryo-sac development in *Enothera muricata*. Competition between the megaspores at the chalazal end and those at the micropylar end in the formation of the embryo-sac. In other ovules only the megaspore at the micropylar end (the uppermost cell) develops as in *O. Hookeri* (normal). (Renner, 1921.)

produces pollen carrying all the possible combinations of factors and complexes, with the exception of **Bm** *flavens* but embryo-sacs of this constitution may be formed. This shows that the complex **Bm** *flavens* is viable in the pollen of the parent *suaveolens*, but that it is inviable in the pollen of the hybrid.

In the *rigens-velans* hybrid resulting from the cross *muricata* \times *Lamarckiana* the factors **Str** *vs.* **str** segregate. It is found that there is only 25% active pollen and that only the combination **Str** and *velans*, *i.e.*, the paternal complex, is active.

Certation. In passing, it should be mentioned that de Vries

(1913), Renner (1914, 1917, 1921 *a*), Davis (1926), Heribert-Nilsson (1925) and Hiorth (1926), show that there are several places in the life cycle where certation between the gametes or zygotes bearing different complexes can be observed. For example, de Vries found that *læta* and *velutina* sometimes appeared from the cross, *Hookeri* × *Lamarckiana* not in the ratio 1 : 1, but ranged from the extremes 7% *læta* to 68% *læta*. Renner (1919 *a, b*) and Hiorth (1926) found that if a small amount of pollen is used, *læta* appears in 22%—42%, but with normal pollination there is 9%—17% *læta*. Both pollen germination and pollen tube growth of *gaudens*-carrying pollen (giving *læta* with *Hookeri*^h) is less than that of *velans* pollen (giving *velutina* with *Hookeri*^h). Heribert-Nilsson had found that pollen of *Lamarckiana* which carried the factor **R** for red nerves grew faster than pollen carrying **r** for white nerves. Hiorth further analysed this and other cases.

	<i>læta</i> .	<i>velutina</i> .
<i>Hookeri</i> × <i>Lamarckiana</i> , white-nerved (rr)—		
sparse pollination	40	56
normal	30	148
<i>Hookeri</i> × <i>Lamarckiana</i> , red-nerved (Rr)—		
sparse pollination	34	111
normal	31	248

It will be noticed that in the second group of crosses the proportion of *velutina* is greatly increased.

	R <i>velutina</i> (red nerves).	r <i>velutina</i> (white nerves).	<i>Læta</i> .
<i>Hookeri</i> × <i>Lamarckiana</i> red-nerved (Rr) totals—			
sparse pollination	127	125	90
normal pollination	336	228	744

The above results indicate that *velans* pollen bearing the factor **r** grows faster than *gaudens* but more slowly than *velans* bearing the factor **R**. There is a difference in the rates of growth of *gaudens* pollen bearing the **R** and **r** factors respectively, but this is not so

noticeable as in the case of *velans*. With sparse pollination the *lata* plants segregated 36 Rr to 54rr. By separating the zygotes from the top and bottom halves of the ovary Hiorth found that in sparse pollination r *gaudens* fertilised almost all the eggs in the upper half of the fruit. These pollen tubes reach the ovule more quickly than pollen tubes bearing the other three genetic contents. Contrary to the above relationships between R and r *velans*, it is found that R decreases the growth rate of *gaudens* as compared with r.

In the hybrid *velans-curvans* resulting from the cross *O. Lamarckiana* × *muricata* the pollen bearing *curvans* can be distinguished from those bearing *velans* by their types of starch grains (see above). It has been observed that the *curvans* type does not grow as fast as the *velans*. Using pollen from the hybrid on the short-styled flower of *O. muricata* a number of *curvans* pollen tubes reach the ovule, but using the same pollen on the longer-styled flower of *O. Lamarckiana* only the *velans*-bearing pollen tubes reach the ovules.

Davis has shown that the pollen tubes from *O. brevistylis*, which is a derivative of *O. Lamarckiana*, grow more slowly than those bearing the normal *velans* or *gaudens* complexes. Species of *Oenothera*, therefore, exhibit to an extreme degree, gametic and zygotic elimination and certation. It is only in the last two or three years that a plausible theory for the origin of these phenomena has been made.

THE FACTOR COMPLEX THEORY

Renner (1917, 1919 a, b, 1921 a) put forward the factor complex theory which has been accepted by almost all workers in the field of *Oenothera*. It is indeed more than a theory, since it is a statement of fact. The heterozygous species of *Oenothera* produce two types of gametes that are apparently distinct and which differ in a number of closely coupled factors. The stability of the complex throughout many generations is at present exceptional among plants or animals. It should be pointed out that the "factors" which constitute the distinctive effect of the complex upon the phenotype are probably mendelian factors, but generally there is no means of isolating them, since their allelomorphs cannot be identified.

Certain examples are instructive in showing that the constancy of

these complexes depends on a mechanism which has been highly specialised in *Ænothera* by the action of natural selection. For the recognition of the complex, Renner gave names to the gametic complements of the *Ænothera* species. Below are given a few of these complexes in well-known species of *Ænothera*, together with an indication as to whether they are functional on the female or male side or on both.

	functioning in egg.	functioning in pollen.
<i>O. Lamarckiana</i>	<i>velans-gaudens</i>	<i>velans-gaudens</i>
<i>O. biennis</i>	<i>albicans-(rubens)</i>	<i>(albicans)-rubens</i>
<i>O. suaveolens</i>	<i>flavens-albicans</i>	<i>(albicans)-flavens</i>
<i>O. muricata</i>	<i>rigens-(curvans)</i>	<i>curvans-(rigens)</i>
<i>O. cruciata</i>	<i>pingens-(flectens)</i>	<i>(pingens)-flectens</i>
<i>O. strigosa</i>	<i>deprimens-(stringens)</i>	<i>stringens-(deprimens)</i>

The complexes in brackets are inviable.

It will be noticed in the above list that *O. biennis* and *O. suaveolens* have the complex *albicans* in common, and it has been found that

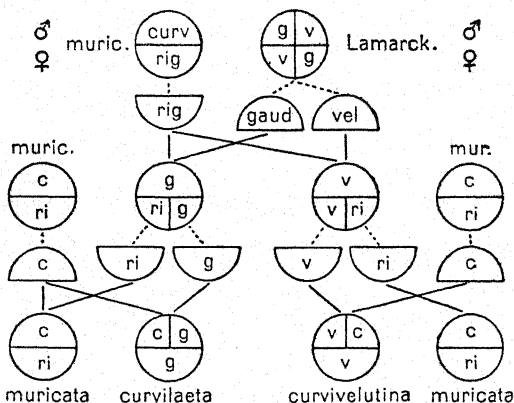
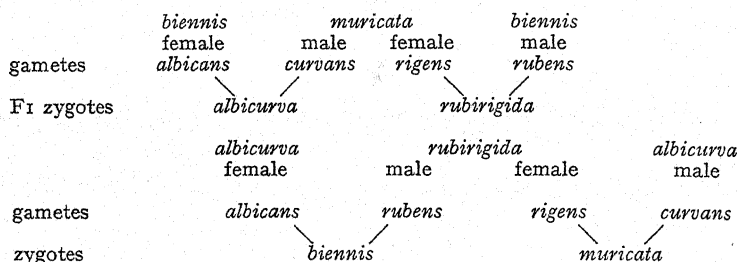


FIG. 48.—Scheme of the reciprocal crosses between *Ænothera muricata* and *O. Lamarckiana* and of the back cross of *O. rigidula* and of *O. rigidivelutina* to *O. muricata* ♂. (Renner, 1929.)

the complexes *rubens* and *gaudens* are very similar in character. The occurrence of the same complex in two or more species has been reported in numerous cases. It has also been found that almost all species of *Ænothera* can be hybridised, giving fertile F_1 s if the genom

is not antagonistic to the plasma. A diagrammatic explanation of the reciprocal crosses between *muricata* and *Lamarckiana* is given in Fig. 48.

The above complexes have been recognised by the behaviour of the species in several species hybrids. The following diagram illustrates the behaviour, due to gametic elimination, of the reciprocal crosses between *muricata* and *biennis*.



The F₁s of the reciprocal crosses differ in a considerable number of characters and may be regarded as two new distinct types. On selfing they do not segregate for *biennis* or *muricata* characters, but breed true for a considerable number of their characters. When, however, the two F₁s are again intercrossed reciprocally, the original species *biennis* and *muricata* are recovered.

The products of a particular cross can be postulated on the basis of experience gained from the use of the parental species in other crosses. Thus it is known that *Lamarckiana* produces two types of gametes, *velans* and *gaudens* on both male and female sides and that *suaveolens* produces functional *albicans* and *flavens* in the egg while only *flavens* is functional in the pollen. In the cross, *suaveolens* × *Lamarckiana* four types are therefore expected in the progeny ;

velans — *albicans*,

(1) *albivelutina*

gaudens — *albicans*,

(3) *albilæta*

velans — *flavens*,

(2) *flavivelutina*

gaudens — *flavens*,

(4) *flavilæta*

The cross *biennis* × *Lamarckiana* gives *albivelutina* and *albilæta* as in the previous cross. The reciprocal cross *Lamarckiana* × *biennis* only gives *rubivelutina* (also known as *fallax*). The expected type

resulting from the fusion of *gaudens* and *rubens* is inviable. Renner (1917) showed that the zygote in the presence of the *r* factor, only reached the stage where there were one or two cells in the embryo and a diseased endosperm, a behaviour comparable in fact to the homozygote (*gaudens-gaudens*).

Both types (*gaudens-rubens* and *gaudens-gaudens*) in the presence of *R* may develop a many-celled embryo before death. Other work indicates that *rubens* and *gaudens* complexes are similar.

It has been pointed out that the heterozygous species of *Ænothera* behave as if they consisted of two gametic complexes. These complexes cannot exist as such in the homozygous state without some change in the genetic properties of the complex. It was realised by the earlier workers that the differences between the complexes of one species must be controlled by many factors. There was little reason to believe that the factors in one complex were necessarily allelomorphic to those in the opposing complex. Some workers suggested that the factors of one complex were close to one another on one chromosome and therefore rarely, if ever, crossed over. We shall see later that chromosomal linkage (catenation) and not genetic linkage is the real explanation of the general non-segregation of the component factors which differentiate one complex from another.

Lethal Factors. To account for the non-survival of homozygotes and for the inviability of gametes Davis (1915), de Vries (1917), Muller (1917, 1930 *a, b*), Morgan (1919), Shull (1923), *et al.* suggested that lethal factors were present.

Heribert-Nilsson (1912) found that on selfing *O. Lamarckiana* segregation of the allelomorphic factors *R* for red nerves *vs.* *r* for white nerves was 2 : 1 in place of 3 : 1. Renner (1914) also found that only 50% of the embryos in *O. Lamarckiana* were sound and suggested that the formula for the heterozygous red-nerved plants was *RrLl*, while that for the recessive white-nerved plants was *rrLl*: all embryos containing *RR* or *LL* or *ll* die. With this hypothesis only the plants of the constitutions *RrLl* and *rrLl* survive out of the 16 genotypes in a dihybrid segregation from selfing. The ratio of *RrLl* to *rrLl* is of course 4 : 2. Hence in this heterozygote *Rr*, the ratio of normal to lethal embryos is 6 : 10, which

approximates to the 1 : 2 ratio found by de Vries (1913), while the white-nerved individuals will have 50% inviable embryos through the lethality of LL and ll. Renner (1925) points out that L and l should not be considered to be mendelian factors in the Morgan sense, but that they represent the sum total of the genotypic constitution of each complex in one respect. (Renner supposed that besides the factors which segregated normally there were others which controlled the definite characteristics of the complex.) They are representatives of Renner's "rest." In passing, it should be mentioned that generally all the mendelian factors which are included in the first linkage group of *Ænothera*, behave in segregation as if closely linked to lethals of the complex.

Balanced Lethal Mechanism. Muller (1917), in a paper on an *Ænothera*-like case in *Drosophila* and again in 1928 and 1930 a, put forward the theory of balanced lethals to account for the puzzling phenomena in *Ænothera*. The homozygote Beaded wing in *Drosophila melanogaster* is a dominant lethal, and hence the ratio obtained in crossing two heterozygotes is usually, 2 Beaded : 1 normal-winged individuals. By artificial selection Muller isolated a strain which bred nearly true for Beaded wing, with the exceptional occurrence of a normal fly. Nevertheless the constant Beaded wing line was heterozygous for Beaded, since it gave a 1 : 1 ratio on crossing to normal (see p. 53). Muller found that the constancy of the Beaded strain was due to the appearance of a lethal factor l on the third chromosome which carried the normal allelomorph to Beaded at a locus close to Beaded. The constitution of the strain

of flies was therefore $\frac{\text{Bd L}}{\text{bd l}}$, which, when bred from would give three

classes of flies, homozygous Bd L and homozygous normal bdl, both of which would die, and the third class similar to the heterozygous parents. The rare occurrence of a cross-over between the loci Bd and L would give normal flies without the lethal factor. In this experiment Muller also found that a suppressor of crossing over was present. This of course would further aid the true breeding potentialities of the heterozygous strain. Similar cases in *Drosophila*, *Antirrhinum* and maize have since been reported by other workers (see p. 53).

Under the influence of a balanced lethal mechanism any true factor mutation would be preserved in the heterozygous condition and thus free from any effect of natural selection towards its elimination. Therefore, once established, the balanced lethal mechanism would favour the accumulation of recessive factors in a latent condition. Any mutations which favoured the support of the balanced lethal mechanism, such as suppressors of crossing over, also would be favoured. Hence new characteristics would be formed by factor mutation in one complex and not in the opposing complex. The appearance of a rare segregate or mutant of de Vries was thus thought to be due to the occasional crossing over between the balanced lethals and a particular character determiner. This, and the foregoing hypothesis, were put forward on orthodox grounds without a suspicion that the behaviour of the chromosomes of *Ænothera* was dissimilar to that of other plants. Muller supposed that the lethals were linked to the factors controlling the special complex differences between one chromosome and its homologue.

Ænothera Lamarckiana gives rise to the form *nanella* in about 0.3% of cases during eight generations of selfing (de Vries). This *nanella* form appears to be governed by a single factor difference from normal *Lamarckiana*. A factor *n* for dwarfness is carried by the *gaudens* complex, but it is not normally present in the *velans* complex, therefore all *Lamarckiana* plants are heterozygous *Nn* and tall, since the homozygotes *gaudens* and *velans* are both lethal. If a rare cross-over takes place between the *gaudens* and *velans* complex in such a way that the recessive factor *n* is transferred to *velans* the mutant *nanella* would appear through the fertilisation of that *velans* gamete (called *nanovelans*) by a *gaudens* gamete containing *n*. When this mutant *nanella* (*gaudens-nanovelans*) is crossed to other species it may or may not segregate. The reasons for non-segregation are (1) the opposing complex in the new hybrid contains no recessive factor *n* and (2) the *nanovelans* complex enters into a new balanced lethal system with the different complex.

For example, *O. biennis* × *O. Lamarckiana nanella* gives the hybrid (*albicans-nanovelans*), which is tall and does not segregate on selfing. But the cross *Lamarckiana* × *biennis* (*rubens-nanovelans*) is dwarf and is homozygous for *n* (*rubens* is similar in constitution to

gaudens). From the cross *muricata* \times *Lamarckiana nanella* the F_1 (*rigens-nanovelans*) is tall and segregates in the F_2 . This is possibly due to the fact that in *rigens-nanovelans* crossing-over may take place more easily between the balanced lethals and *nanella* than in *albicans-nanovelans*.

De Vries (1913, 1918) and Shull (1923) showed that the alternative characters, yellow and sulphur flower colour, were allelomorphic in *suaveolans* and *biennis* (S s). When the cross S female \times s male was made the F_1 was yellow (s). The reciprocal cross was sulphur (S).

The F_2 did not segregate but, like the F_1 , had the colour of the male parent. The suggestion is made that S for yellow is linked to an egg lethal and s for sulphur is linked to a pollen lethal. Therefore functional eggs only carry s and functional pollen only carry S. Shull obtained cross-overs between these factors and the lethals, and therefore obtained plants in which the colour followed the opposite parent, and he also obtained them free from lethals. In this latter case the inheritance was normal.

Catenation. Gates (1908) first called attention to the fact that the chromosomes of *Oenothera* had a tendency to remain in groups of more than two chromosomes at the reduction division. Later Cleland (1922, 1923, 1925), Emerson (1924), Oehlkers (1926), Håkansson (1926) and others showed the correlation between the heterozygous species of *Oenothera* and ring formation of the chromosomes. As a result of much painstaking work between 1922 and 1928 it was discovered that there was a definite arrangement of the chromosomes in the ring which could consist of an even number of from four to fourteen chromosomes, with the remainder as bivalents. Sometimes two or more small rings were formed instead of bivalents (see p. 297). It was found that different hybrids had different but constant (with few, but important, exceptions) numbers of chromosomes in the ring and that those hybrids with large rings had more of the mendelian factors linked to one another than in the hybrids with smaller rings of chromosomes.

It was thought that the maternally and paternally derived chromosomes alternated in the ring at the reduction division so that paternal chromosomes went to one pole and maternal to the other. The telosynaptic hypothesis, now replaced by the parasynaptic

hypothesis, aided this interpretation to a small extent, but it hindered the standpoint now adopted that besides having an alternate arrangement in the ring the paternally and maternally derived chromosomes have a definite position in relation to each other.

If all the paternal chromosomes in the ring went to one pole and all the maternal chromosomes to the other, the complexes contained in each set would not be mixed and would remain as entities as long as the ring mechanism continued unchanged. Cleland and Oehlkers (1929) mention 20 species hybrids in which (1) the hybrids varied greatly in the number of chromosomes in the ring as compared with the parents, (2) two factors showed different linkage relationships in different hybrids, (3) where a ring consisted of a large number of chromosomes, segregation was at a minimum, but where few chromosomes were involved in the ring there was clear-cut segregation. Cf. Oehlkers (1926), Rudloff (1929), Gerhard (1929) and Hoeppener and Renner (1928).

Structural Hybridity. The reader will at once observe that these facts in *Ænothëra* are similar in kind, but of more extreme degree, to those described earlier (see p. 264) in *Datura*, *Pisum*, *Zea*, *Campanula* and other plants of structural hybrid nature. Darlington (1929 a, 1931 b), Cleland and Blakeslee (1930), Håkansson (1929 b) and Muller (1930) have adopted the structural hybridity theory for *Ænothëra* with far-reaching results.

The main points of the theory will be discussed below, but a much fuller contribution is made by Darlington (1931 b) in a masterly and condensed treatise.

There are three main phenomena in *Ænothëra* which should be associated together, (1) balanced lethal mechanism, (2) ring formation, (3) association of many genetical factors into one linkage group.

In species with ordinary pairing resulting in bivalents, the presence of a single balanced lethal system, such as is supposed to exist in *Ænothëra*, can control one linkage group, i.e., the factors carried by one pair of chromosomes at most. Further, it reduces the fertility of the plant by one half. If the heterozygosity of such a species is to be preserved in respect of all the chromosomes by a balanced lethal mechanism the fertility would be $\frac{1}{2}^7$, a negligible

quantity. Suppose that a balanced lethal mechanism existed on one pair of chromosomes and segmental interchange took place between that pair and a non-homologous pair; the mechanism would then control four chromosomes in place of two without further reducing the fertility. Naturally, any increase in the number of chromosomes in the ring following hybridisation or by internal interchange followed by selfing, would be favoured by natural selection. Renner (1927), Darlington (1929 *a*).

A species forming bivalents of the constitution, $AB\ AB, CD\ CD, EF\ EF, GH\ GH, KL\ KL, MN\ MN, OP\ OP$, can, by six interchanges between non-homologous chromosomes, give rise to a type with a ring of fourteen chromosomes, $AB\ BC\ CD\ DE\ EF\ FG\ GH\ HK\ KL\ LM\ MN\ NO\ OP\ PA$. Such a type would give rise to gametes containing paternally or maternally derived chromosomes, namely, $AB\ CD\ EF\ GH\ KL\ MN\ OP$ and $BC\ DE\ FG\ HK\ LM\ NO\ PA$, *i.e.*, two complexes.

It will be seen that in the ring of fourteen, one chromosome is homologous at opposite ends with ends of two different chromosomes; thus the *C* segment of *BC* is homologous with the *C* segment of *CD* and the *B* segment with the *B* segment of *AB*.

Differential Segment. The cytological findings (Darlington, 1931 *b*) show that chiasma formation takes place between homologous segments and hence crossing-over may occur between factors placed on the terminal segments of these chromosomes. Factors in these segments may thus pass from one complex to another. Pairing is usually restricted to the ends of the chromosomes and it is probable that the middle portion is not homologous with any part of either of the adjacent chromosomes. In any case, crossing-over does not seem to occur normally in the middle part of the chromosomes.

Various genetical and cytological data indicate that the middle portion is of appreciable size and Darlington suggests that the causes underlying the differences in properties of opposing complexes together with the so-called balanced lethal mechanism lie in this region of the chromosomes. Each chromosome therefore consists of two terminal segments which pair with terminal segments of two other chromosomes and one median differential segment which is

supposed to contain the factors controlling the balanced lethal mechanism and the differences between the complexes.

The differential segments could be formed through segmental interchange in the following manner. In the original bivalent-forming line $AB\ CD$ two parts of the B segment can be represented as X and B_1 , X representing the inner portion of the B segment, *i.e.*,

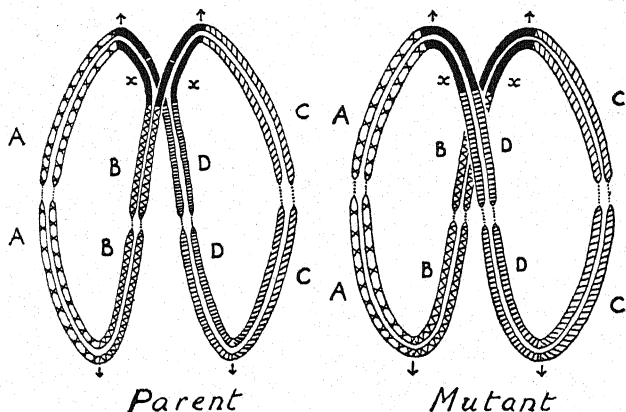
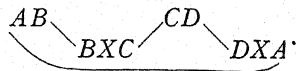


FIG. 49.—Diagram showing the origin of a "lethal" system, "complex" system, and ring formation by crossing-over between translocated and non-translocated interstitial segments " x ." The parent structural hybrid plant of constitution AB, AxB, CD, CxD gives a mutant with a ring of four of the constitution $AB, Dx C, CD, Dx A$. The only viable gametes that can be produced by such a system are (i.) deficient in x , and (ii.) reduplicated in x . They differ in segmental constitution and, meeting will produce the "mutant" structural hybrid with a ring of four. The points of crossing over in the x segments of two chromatids in the parent are marked by a gap. Terminilisation has taken place and been arrested by the change of homology. (Darlington, 1931 *b*.)

the line is $AXB_1\ CD$, etc. By translocation the portion X may be transferred to the CD chromosome (CXD), and a different line, $ABCXD$, will be created. The hybrid between these two lines will be of the constitution, $AXB\ CD\ CXD\ AB$. Fig. 49 shows the configuration that would arise if a chiasma were formed in the X segments in such a hybrid.

Segmental Interchange. Somewhat similar configurations have actually been observed in *Enothera* by Darlington (1931) and in

Pisum by Sansome, E.R. (1932). See Fig. 19. These have been considered on p. 90. Chiasma formation in the *X* segment will produce the crossed over chromatids *AXD* and *BXC*. A gamete containing *AXD* and *BXC* on uniting with a gamete from the ancestral line *AB CD* will give a form having a ring in which the middle portions of the chromosomes are distinct



If reduplication or deficiency of the *X* segment does not cause gametic inviability a condition may arise in which only zygotes of the constitution *AXD BXC AB CD* are functional. In other words the balanced lethal mechanism may be constituted not by factors but by the balance of factors contained in the differential middle segments. Thus homozygotes (*AXD BXC AXD BXD*) and (*AB CD AB CD*) may be non-functional through the two-fold reduplication or deficiency of the *X* segment.

Renner's "Rest." That the contents of the differential segments, or, in genetical terms, the "Rest" of Renner are diverse, is indicated by the fact that some heterozygotes such as *biennis*, do not give viable homozygotes, while others such as *Lamarckiana* may give rise, as the result of interchange, to normal homozygotes such as *deserens*, *blandina*, etc. Others, again, such as the heterozygote of the complexes (*truncans-gaudens*) give rise to crippled plants, which are presumably homozygotes (Cleland and Oehlkers, 1929).

The hybrid from *suaveolens* × *biennis* produces a functional homozygote (*flavens-flavens*) known as *lutescens* (Renner, 1927) through crossing over between *flavens* and a complex with which it is not usually in association, namely *rubens*. This homozygote has seven pairs of chromosomes.

Renner (1921 b) had suggested that where one complex, such as *curvans* in *muricata*, is more viable in the pollen, any greater success of the other complex in the embryo-sac production will be favoured by the greater fertility of the plant. Since the distinctive features of the two complexes are suggested to be in the differential segments which do not form chiasmata, and which from the foregoing discussion presumably will differ quantitatively and qualitatively in their genetical material, it can be seen that the action of natural

selection on the materials in one differential segment does not interfere with that of another. Hence the separation of the differential segments from the pairing segments allows new factors to arise independently for each complex through natural selection. It is therefore possible to have widespread interspecific hybridisation in the genus *Ænothera*, since the ends of the chromosomes are homologous throughout the group while the middle segments may not be.

It can be seen therefore that the view sometimes held, that a species hybrid is characterised by an anomalous behaviour compared with that of the parent species, is erroneous. In *Ænothera*, two heterozygous species may give rise through hybridisation to a homozygous seven bivalent "hybrid" which is similar in its genetical behaviour to the many non-ring-forming plants that have been studied. It will be realised that the homozygous derivatives of a ring-forming heterozygote might show chiasma formation in the middle segments as well as the end segments of the chromosomes. But in derivatives of hybrids such as (*flavens-subcurvans*), Rudloff (1929) or of the half-mutant forms such as *rubrinervis*, which arises from *Lamarckiana* and gives rise to the homozygous mutant *deserens*, it would be expected that differentiation would be negligible, since the mutant homozygote would have the direct descendants of the chromosomes of one complex in the heterozygote. (In the hybrids between *suaveolens* and *strigosa* (*flavens-strigens*) and between *purpurata* and *suaveolens* (*flavens-purpurata*^b) which have seven pairs of chromosomes, one might find that the middle segments had differentiated from the common ancestral type.)

It should be possible to study the amount of differentiation of the middle segments of the complex that has taken place during isolation from the time that it was contributed in its ancestral form to both of the heterozygotes.

The second class of mutation arising through the rearrangement of the genetical material illustrates the complicated phenomena to be expected in a ring-forming diploid organism.

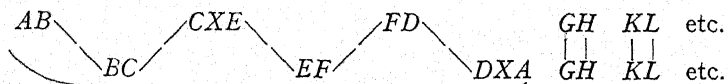
CROSSING OVER IN THE MIDDLE SEGMENTS

Darlington (1931b) and Sansome, E.R. (1932) have observed figure-of-eight configurations of chromosomes in *Ænothera* and

Pisum respectively. This figure-of-eight configuration arises through the formation of a chiasma in a middle segment, the *X* segment, of two otherwise non-pairing chromosomes in a ring. This middle segment has different homologies from the end segments as postulated earlier (see Fig. 49, p. 289).

Let us consider a ring of six chromosomes in *Pisum* which arose from crossing two plants each of which gave a ring of four chromosomes when crossed to normal. There must be a chromosome in common in the two rings. Thus the rings of four can be represented as $AB \searrow BC \swarrow CD \searrow DXA$ and $EF \searrow FD \swarrow DC \searrow CXE$.

Interchanges in the normal line $AB\ CD\ EF\ GH$, etc., could have taken place between CD and AB on the one hand, and CD and EF on the other hand to give the other two lines. The *X* segment may have been formed as a result of these interchanges having taken place at different levels on the CD chromosome. If we divide the D segment into four portions, 1, 2, 3, 4, with 1 nearest the C segment and call the CD chromosome $C1, 2, 3, 4$, then one interchange between AB and $C1, 2, 3, 4$ may result in e.g. $A1, 2, 3, 4$, and BC , while the other interchange between EF and $C1, 2, 3, 4$ may be, e.g., $F3, 4$ and $C1, 2, E$. Representing the segments 1, 2 by X and 3, 4 by D , we obtain $AXD\ BC$ and $FD\ CXE$. On crossing these two plants with rings of four chromosomes, four possible types can be obtained in the ratio, one normal line : two lines with a ring of four corresponding to the original rings of four : 1 plant with a ring of six. This ring of six is arranged thus :—

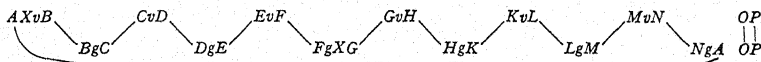


in which the top line represents the gametic complement derived from one parent and the lower line that derived from the other.

In a certain proportion of cases, depending upon the position of the *X* segment relative to the other segments, a chiasma is formed between the *X* segments in chromosomes AXD and CXE . This gives rise to the figure-of-eight configuration which is important in several respects. On studying the chromatids involved in the

chiasma at the *X* segment it is seen that two correspond to the original chromosomes *AXD* and *CXE*, while *two are constituted by CXD and AXE* (see Fig. 19).

For our present purpose, it is necessary only to consider the consequences of such a figure-of-eight configuration in a ring-forming species of *Ænothera* such as *Lamarckiana*. *Ænothera Lamarckiana* gives rise to many forms, the origin of many of which can be explained by the above theories. The ring of twelve chromosomes and one bivalent of *O. Lamarckiana* can be represented by



v and *g* represent the differential segments which presumably carry the characteristics of the complexes *velans* and *gaudens* respectively together with the so-called lethals (the origin of the *v* segment is unknown), while the two *X*'s represent two homologous median segments in different chromosomes.

Origin of Half-Mutants. By crossing-over in the *X* segment four different chromatids involving the *X* segment will be obtained, namely *AXvB GXvB GXgF AXgF*. Segregation of these chromatids (with a numerically even number of chromosomes) will be non-disjunctional for two of the four and disjunctional for the other two according to the orientation of the ring. In the diagram (Fig. 19) the two crossed-over-chromatids will disjoin regularly, while the original chromatids will show non-disjunction at one end. Hence with this method of disjunction the resulting gametes with the new types will probably be viable and those with the original types inviable.

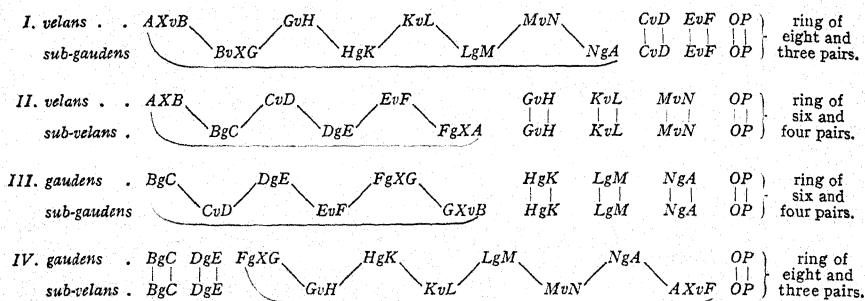
The original gametic complements on *O. Lamarckiana* were :—

<i>velans</i>	.	<i>AXvB</i>	<i>CvD</i>	<i>EvF</i>	<i>GvH</i>	<i>KvL</i>	<i>MvN</i>	<i>OP</i>
<i>gaudens</i>	.	<i>BgC</i>	<i>DgE</i>	<i>FgXG</i>	<i>HgK</i>	<i>LgM</i>	<i>NgA</i>	<i>OP</i>

After crossing-over in the *X* segment and regular disjunction for the crossed-over chromatids there results :—

<i>sub gaudens</i>	<i>GXvB</i>	<i>CvD</i>	<i>EvF</i>	<i>AgN</i>	<i>MgL</i>	<i>KgH</i>	<i>OP</i>
<i>sub velans</i>	<i>BgC</i>	<i>DgE</i>	<i>FgXA</i>	<i>NvM</i>	<i>LvK</i>	<i>HvG</i>	<i>OP</i>

These gametic complements on meeting unchanged *gaudens* or *velans* will give rise to four different heterozygotes with different chromosome configurations.



For example, *O. Lamarckiana* with a ring of twelve and one pair of chromosomes produces *O. rubrinervis* with a ring of six and four pairs in about 0.1% of the progeny (Cleland, 1925). *O. rubrinervis* is a so-called half-mutant since it produces the fertile mutant *deserens* in $\frac{1}{4}$ of the seed. The remaining $\frac{3}{4}$ of the seed is made up of $\frac{1}{2}$ *O. rubrinervis* and $\frac{1}{4}$ inviable embryos (de Vries, 1918; Cleland, 1925).

The complexes of *O. rubrinervis* can be represented as *sub-velans-pænevelans*. Renner (1927) concluded from genetical analysis that *sub-velans* arose through crossing over between *velans* and *gaudens*, since it exhibited qualities of both, while Hoeppener and Renner (1928) suggested that *pænevelans* and *velans* did not differ greatly when combined with other complexes (except with *sub-velans*). The second of the formulæ given above (*velans-sub-velans*) agrees well with the description of *O. rubrinervis*, while *subvelans-subvelans* would give a form with seven bivalents in which the differential segments of *gaudens* and *velans* have been recombined. This form corresponds to *deserens*. The form *velans-velans* constitute the inviable embryos while half the seed will again reproduce *O. rubrinervis*.

The half-mutants, *erythrina*, *blandina*, *rubrisepala* probably arose in a similar fashion, either as the result of crossing over between the same differential segments or between those of other chromosomes.

Erythrina gives rise to the segregating factor for *fragilis*. This is expected if the factor for *fragilis* is carried on the X or differential segments which become homozygous, and pair in a similar way to the terminal segments. In the formula above it will be seen that the segments *Xv* of chromosomes *AXvB* and *BvXG* are continuations of pairing segments whereas in the ancestral *velans-gaudens* arrangement they are isolated from one another.

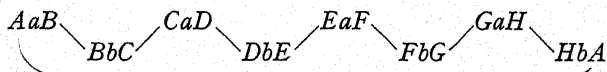
The above theory of the origin of half-mutants and secondary full mutants agrees with the facts in (1) the frequency of occurrence of the half-mutant should be constant, since it is a function of crossing over between definite lengths of chromosomes.

(2) The particular mutant at every appearance should have the same characteristics.

(3) The complexes of the mutant should be unchanged and consist of a mixture of the parental complexes.

(4) One "half and half" complex survives as a homozygote, such as *subvelans-subvelans*, while the other dies, *subgaudens-subgaudens*. Through crossing-over, the lethal factors of *velans* have been transferred to the *gaudens* complex, giving rise to viable *subvelans* and lethal *subgaudens*. In a trisomic form, one chromosome is left free to pair with any other homologous part, therefore exceptional crossing-over may take place more frequently. It follows therefore that half-mutants will be produced more frequently and in greater variety in the trisomic forms than in a diploid. This is probably the case in *O. nitens*, a trisomic which gave rise to 6 mutants out of 100 seedlings, of which one was a half-mutant *distans* (de Vries, 1923).

Mass Mutants. Interchanges between segments within one complex also would give rise to mutant forms. A probable case is that in which the segments *B* and *F* interchange in a ring of eight.



to give a viable gamete with one new type of arrangement which with the complementary complex will give



i.e., the new form will have unchanged physiological properties but the pairing properties will be changed (two rings of four and three bivalents); the new form will be indistinguishable from the old but naturally the range in gametic output is increased. The chromosomes of one ring will disjoin independently from that of the other, therefore there are four possible gametic types. The sudden appearance of several new forms, though possible in the immediate progeny of this plant, is more likely to occur in later generations.

Discussion. On the above theory of the origin of ring forming species of *Oenothera*, together with the necessary assumption of specificity of pairing, one is able to explain the known facts of behaviour and to make predictions of the configurations of chromosomes to be found in hybrids between two known species.

Analysis and prediction have been made by Cleland and Blakeslee (1930), Cleland (1931) and Darlington (1931 *b*).

The following table of configurations of several species has been adapted from Darlington's more extensive list in which the authorities for each will be found :—

Ring of Fourteen.

- O. muricata*, *curvans-rigens*.
- O. strigosa*, *deprimens*—*stringens*.
- O. (R) biennis* × *Hookeri*, *albicans-Hookeri*^h.
- O. biennis* × *O. Lamarckiana*, *albicans-velans*.
- O. Lamarckiana* × *suaveolens sulfurea*, *albicans-velans*.
- O. Lamarckiana cruciata* × *strigosa*, *gaudens-strigens*.
- O. suaveolens* × *Hookeri*, *albicans-Hookeri*^h.

Ring of Twelve and One Pair.

- O. Lamarckiana* and cross-over mutants, *gaudens-velans*.
- O. suaveolens*, *albicans-flavens*.
- O. Lamarckiana* × *biennis fallax*, *rubens-velans*.
- O. biennis* × *suaveolens* and reciprocal, *albicans-flavens* and *rubens-flavens*.
- O. Lamarckiana* × *suaveolens sulfurea*, *gaudens-flavens*.
- O. suaveolens* × *strigosa* and reciprocal, *albicans-strigens*, *deprimens-flavens*.
- O. purpurata* × (*Lamarckiana* × *purpurata*), *purpurata-velans*.

Ring of Eight and Six Pairs.

- O. biennis*, *rubens-albicans*.
- O. biennis* × *Lamarckiana*, *albicans-gaudens*.

Ring of Ten and Two Pairs.

- O. biennis* × *Hookeri*, *rubens-Hookeri*^h.
- O. Hookeri* × *Lamarckiana*, *Hookeri*^h-*gaudens*.
- O. Lamarckiana cruciata* × *strigosa*, *deprimens-velans deprimens-gaudens*.
- O. purpurata* × *Lamarckiana*, *purpurata-gaudens*.

Rings of Six and Four and Two Pairs.

- O. biennis* × *muricata*, *albicans-curvans*.
- O. Lamarckiana* × *strigosa*, *velans-strigens*.

Two Rings of Four and Three Pairs.

- O. Hookeri* × *Lamarckiana*, *Hookeri*^h-*velans*.
- O. Lamarckiana* × *suaveolens*, *sulfurea*, *velans-flavens*.

Ring of Six and Four Pairs.

- O. rubrinervis*, *pænevelans-subvelans*.
- O. erythrina*.
- O. mut. sulfurea*.

Ring of Four and Five Pairs.

- O. franciscana*.
- O. Hookeri* × *suaveolens*, *flavens-Hookeri*^h.
- O. biennis* × *muricata*, *albicans-curvans*.
- O. suaveolens* × *strigosa*, *flavens-strigens*.

Seven Pairs.

- O. Hookeri*.
- O. blandina* ex *Lamarckiana*.
- O. deserens* ex *Lamarckiana*.
- O. suaveolens* × *strigosa*, *flavens-strigens*.
- O. purpurata*.
- O. purpurata* × *suaveolens*, *purpurata-flavens*.

Cleland (1931) brings out one consequence of the theory, namely, that those complexes which are genetically closely related yield either bivalents or small rings, when combined with each other, while those with greater differences give larger rings in the hybrids. Hoepfner and Renner (1928) constructed a diagram of the relationships which they found between various complexes on purely genetical grounds. Cleland (1931) superimposed on this diagram

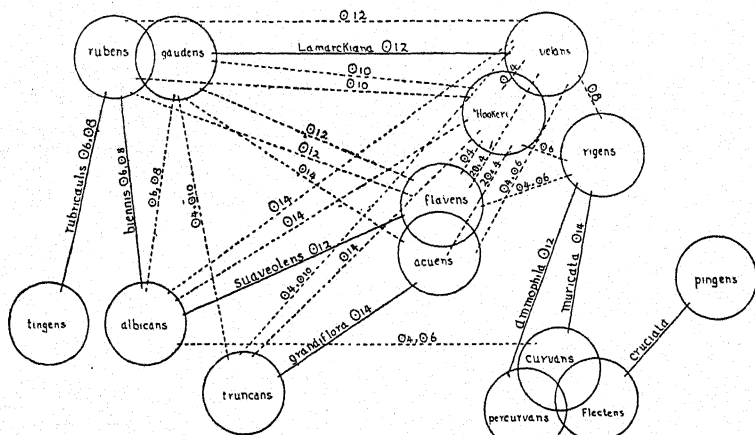


FIG. 50.—Modification of Hoepfner and Renner's diagram showing the genetic relationships between certain complexes of *Oenothera* together with the chromosome configurations produced by the various complex combinations. Solid lines connect complexes associated in spontaneous races. Dotted lines connect complexes associated in artificial hybrids. (Cleland, 1931.)

(see Fig. 50), the configurations known to be produced in the complex combinations. He found that the distances between the complexes on Hoepfner and Renner's diagram corresponded to the size of the ring in the zygote made from the combination of the complexes. Only a slight alteration was required to make the cytological and genetical diagrams agree entirely, namely, that *rigens* be placed as in the diagram further from *velans* and that the position of *velans* and *Hookeri*^h be reversed. It has already been mentioned that *rubens* and *gaudens* are very similar genetically. It has been found that both give similar configurations when

combined with every other complex so far studied. *Hookeri*^h and *velans* are not identical but closely related genetically and give related configurations, e.g. *gaudens-velans* (12) and (2); *gaudens-Hookeri*^h (10) and 2(2); *albicans-velans* (14); *albicans-Hookeri*^h (14); *flavens-velans* (4) and (4) and 3 (2); *flavens-Hookeri*^h (4) and 5 (2), Cleland (1931).

The reason for the above phenomena is not difficult to understand. Closely related complexes probably arose by the same or similar segmental interchanges. By continued isolation in different heterozygotes (such as *rubens* in *biennis* and *gaudens* in *Lamarckiana*) there is opportunity for factor mutations to occur. This does not disturb the pairing properties of the end segments. If the requirements of natural selection have been met in a heterozygous species with a large ring, or two large rings, the products of any segmental interchange between non-homologous segments will not be spread through the population.

Two out of many interesting examples illustrate the possibilities and behaviour of *Enothera*.

When *O. Chicagensis* (*excellens-punctulans*) is crossed with *O. biennis* (*rubens-albicans*) the normal hybrid is *rubens-excellens*. Occasionally, however, *punctulans-rubens* appears in a small proportion of the progeny. When the latter is crossed with *biennis* as female, one of the possible types is *albicans-rubens* or *biennis*. Cleland (1931) reports that this resynthesised species has a ring of six and a ring of eight typical of the original *biennis*.

Gates and Catcheside (1931) intercrossed the homozygous mutants *O. deserens*, *O. purpurata* and *O. blandina*. Each has seven pairs of chromosomes. The cross, *deserens* × *purpurata* gave a ring of four and five pairs, *blandina* × *purpurata* a ring of four and five pairs, *deserens* × *blandina* a ring of six and four pairs.

A start has been made in mapping the chromosomes of *Enothera* and describing the interchanges that have taken place to form the various complexes. Cleland and Blakeslee (1930), Cleland (1931) and Emerson and Sturtevant (1931) have compared the configurations formed in different combinations of the complexes and come to a definite conclusion as to the chromosomes involved.

The following is a list compiled from these authors in which we

have adopted our usual lettering for the segments of the chromosomes in place of the numbers which these authors have used. The arbitrary normal line is *Hookeri*^h with chromosomes therefore labelled *AB CD EF GH KL MN OP*.

<i>Hookeri</i> ^h	.	.	<i>AB CD EF GH KL MN OP</i>
<i>flavens</i>	.	.	<i>AD BC EF GH KL MN OP</i>
<i>velans</i>	.	.	<i>AB CD EH GF KL MN OP</i>
<i>excellens</i>	.	.	<i>AB CD EF GL HK MN OP</i>
<i>strigens</i>	.	.	<i>AD BC EL GH KF MN OP</i>
<i>gaudens</i>	.	.	} <i>AB CP EF GD NL MH OK</i>
<i>rubens</i>	.	.	
<i>albicans</i>	.	.	{ <i>AD CE FH GL KN MP OB or AD GP,</i> etc., Emerson and Sturtevant.
<i>franciscans</i>	.	.	<i>AB CD EF GL HK MN OP</i>
<i>sub-velans</i>	.	.	<i>NMEH FG DL CP OK</i>
<i>sub-gaudens</i>	.	.	<i>MHFE GD NC PO KL</i>

In conclusion, the adoption of the theory of segmental interchange for the origin of ring-forming plants and of the theory of specificity of pairing has revolutionised the views and lines of work on *Oenothera* and other species. All the consequences of the two theories have not been mentioned in this short summary, but it is hoped that it will indicate the trend of thought of cytogeneticists. One consequence, however, should be mentioned. The number of chromosomes allotted to each gamete depends on regular disjunction occurring at the heterotype division. The mechanism of disjunction of rings is of a particular and complicated type, and is expected to produce irregularities more frequently than that governing bivalent separation. Therefore, as expected, we find that polyploid and aneuploid forms are noticeably frequent in *Oenothera*. The gametic output of any heterozygous form of *Oenothera* with more than 14 chromosomes will obviously be varied since the presence of re-duplicated segments will influence the manner of ring formation and of disjunction. It is therefore not surprising that there are many more primary trisomics than the seven expected types (see p. 243). Attempts were made by the earlier workers to apply the complexes of a diploid *Oenothera* to the polyploid derivative. For example, the

Lamarckiana gigas 4x and *semigigas* 3x mutants were supposed to be made up of *gaudens* and *velans*. There were two *gaudens* and two *velans* in *Lamarckiana gigas* and a proportion of two to one in *semigigas*. It was soon found, however, that the complexes lost their identity at the first meiosis of the new form. This is to be expected on cytological grounds, since the configuration of chromosomes will no longer be a ring of twelve and one pair as in the diploid, or two rings of twelve and two pairs expected in the tetraploid. The physiological properties of the gametes produced by trisomics and aneuploids of *Ænothera* are different from organisms which are not structural hybrids, since the variety of the output is large and involves reduplication and deficiencies of differential as well as of pairing segments. Therefore in *Ænothera*, as distinct from most other plants, zygotes with chromosome numbers ranging from 14 almost continuously to 28, 29 and 30 are functional.

Reference should be made to Gates (1928), who has done a considerable amount of work on these forms and to Lehmann (1922) for further information on polyploid *Ænothera*.

LINKAGE BETWEEN GENETIC FACTORS

Renner (1925), etc., and Shull (1923, 1928 *b*, 1929, 1930) came to the conclusion that there were three or four recognisable linkage groups among the *Ænothera* species. Shull enumerates the factors in each group thus: linkage group 1, M m margined *vs.* no margined leaf, N n normal *vs.* nanella habit, S s yellow *vs.* sulphur flowers and P p punctate *vs.* non-punctate stems (nomenclature of Emerson and Sturtevant, 1931). There has been so far no crossing over between the factor for *rubricalyx* buds and punctate stems, therefore the latter authors provisionally make the following allelomorphic series founded on Renner's original factor P.

Pr (the Rh factor of Shull) red hypanthium.

Ps (PStr of Renner, Rc of Shull) *rubricalyx*.

P (Pstr of Renner) striped buds.

p (r of Shull) green buds.

Linkage group 2 includes only the factor for *brevistylis*.

Linkage group 3 consists of **V v** normal *vs.* old gold flower colour, **Bu bu** normal *vs.* bullate leaf and a factor for doubleness. All these factors are strongly linked to one another.

Shull worked with only a limited range of material, including *Lamarckiana*, *biennis* and their derivatives, and Renner points out that in other material the factors of linkage group 1 may be independent from one another. Renner (1928) gives as an example the following diagram of linkages between five factors: **R** for red nerves, **Pm** for margined leaf, **B** for broad leaf, **Sp** for pointed leaf,

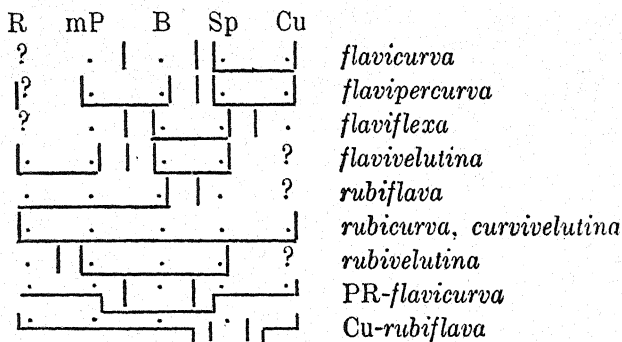


FIG. 51.—Linkages of factors in different *Oenothera* hybrids. Horizontal lines indicate linkage and vertical lines separate factors which are independent. (Renner, 1928.)

and **Cu** for pendulous tip Fig. 51. It will be seen that in *rubicurva*, *rubipercurva* and *curvivelutina* all five factors are linked to one another, but in *flavicurva* **m** and **B** are independent from one another and from the linked factors **Sp** and **Cu**.

Renner (1928), Cleland and Oehlkers (1930), Emerson (1930, 1931 *a, b*), Emerson and Sturtevant (1931), and Sturtevant (1931) realised that the linkage phenomena were due to ring formation. This is, in general, similar to that already discussed in *Pisum*, maize and *Campanula*. But, as Darlington (1931 *b*) pointed out, the linkage map of an *Oenothera* species should be represented as follows (Fig. 52), since the differential middle segments do not normally cross over. Emerson and Sturtevant (1931) identify the

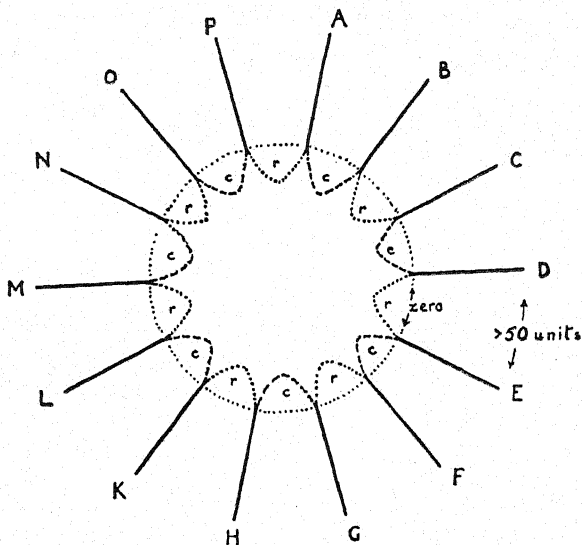


FIG. 52.—Diagram to represent potential crossing-over map in *Enothera muricata* of the constitution.

curvans: A_cB C_cD E_cF G_cH K_cL M_cN O_cP
 rigens: B_rC D_rE F_rG H_rK L_rM N_rO P_rA

c represents the differential middle segments of the seven *curvans* chromosomes, r those of the *rigens* chromosomes. Crossing-over occurs between terminal segments with the same capital letters, not between the c and r segments adjacent to these. The lengths of the interior segments are shown equal and likewise those of the exterior segments, but this is arbitrary, for their lengths must be variable following the occurrence of segmental interchange as a result of exceptional crossing-over within the circle, i.e., between complex differentials. Note: This map corresponds to a constant complex, not to changes of complex with which most crossing-over determinations in *Enothera* are concerned. (Darlington, 1931 b.)

following segments of the chromosomes composing the complements of the species enumerated above with the factors:—

- R in A or B.
- P in C or D.
- Fr in A or D.
- S in C.
- N in C or D.
- V in E or F.

By adopting this view one can account for the occurrence of independence and linkage of the same factors in different heterozygotes and also for the appearance of more than one apparent linkage group in *O. Lamarckiana* with a ring of twelve and one pair. Shull found it difficult to see how the behaviour of the three linkage groups could be harmonised with such chromosome configurations. Other possibilities however must be considered in the light of the new theory of *Oenothera* behaviour.

(1) During the experiments for testing crossing-over, Shull probably used plants with different segment arrangements. Indeed it is known that one race denoted by N, which contains the recessive factors, does have a different segment arrangement from the others. This will necessarily give rise to plants with different configurations in Shull's hybrid from that of the original *Lamarckiana*. (2) His linkage group 3 contains three factors which occupy not more than three units on a chromosome and can be considered to behave as a single unit while linkage group 2 is represented by one factor. The pairing segments must be at least 50 units in length, since they have been found to pair regularly (Darlington, 1931 *b*), and at least one chiasma is required for pairing. If, as Emerson and Sturtevant suppose, the factors of linkage group 1 are on *CD* and of 3 on *EF*, and if those on *EF* are at the distal end of either *E* or *F*, they might easily be more than 50 units from the point of interchange and be still more readily 50 units from any factor on *CD* when both *CD* and *EF* are in one ring.

The following experiments of Emerson (1930, 1931 *a, b*) illustrate well the type of phenomena to be expected in *Oenothera* and the lines along which future work requires to be done.

Oenothera franciscana has 5 bivalents and a ring of four, Cleland (1922), and is genetically homozygous and free from lethals. It contains the dominant factor (*S*) for flower colour and recessive (*gr*) for green bud cones and the dominant normal tall habit (*D*). After crossing *O. franciscana* with *O. biennis* a form *franciscans-sulphurens* arises with green bud cones (*Gr*) and sulphur flowers (*s*) which is otherwise similar to *franciscana* in habit. This form has 50% abortion of pollen and a ring of twelve and one pair, (Cleland, 1923), or a ring of ten and two pairs, (Emerson, 1931 *a, b*).

Franciscans-sulphurens, when inbred, segregates a form, sulphur dwarf, in 3% of the progeny. Sulphur dwarf differs in size and colour of bud cones (d gr), has no gametic lethals and has seven pairs of chromosomes.

Segregation of S : s in the F₁ between *franciscana* and *sulphurens-franciscans* back crossed to *sulphurens-franciscans* is

	S	s
eggs	2,133	821
pollen	370	180

In both cases there is a deficiency of the recessive form. On the other hand the dwarf habit of sulphur dwarf segregates in a 3 : 1 ratio without deficiency. The factor for green cones Gr gr is linked to a pollen lethal, hence in the F₁ of *franciscana* with gr × *sulphurens-franciscans* Gr there were found 537 gr : 0 Gr, and in the reciprocal cross 269 gr : 248 Gr indicating that *franciscana-sulphurea* was heterozygous, Gr gr. The constitution of *O. franciscana* is *franciscans-franciscans*, of *O. franciscana sulphurea* is *sulphurens-sd-franciscans* and of sulphur dwarf is *sd-franciscans-sd-franciscans*.

The factors S_{pl} for splashed bud cones and d for dwarf are almost completely linked in *sulphurens-sd-franciscans*, while in *sulphurens-franciscans* the factors s_{pl} gr and s are closely associated (s_{pl}-gr 3.5% gr-s 4.5%). Hence it is probable that s and d are also closely associated. But in *franciscans-sd-franciscans* s and d are independent. The first two hybrids have rings and the last hybrid has seven pairs of chromosomes. Emerson points out that if these factors are in separate chromosomes which participate in the ring in *sulphurens-franciscans* they will show linkage with one another but not in a form with seven pairs of chromosomes.

CHAPTER IX

INTERSPECIFIC HYBRIDISATION

Galeopsis—Triticum—Nicotiana—Crepis—Viola—Antirrhinum.

THE results of the investigations in different genera by geneticists, cytologists and taxonomists will be summarised in this chapter.

A cursory outline of the genetics of interspecific hybrids will be made in such a way that the new outlook on the species question may be understood. It will also be seen that much monographic work on genera is essential for the understanding of many biological problems of the future.

Galeopsis. Müntzing (1930 *a, b*, 1932 *a, b*) crossed *Galeopsis pubescens* ($2n = 16$) with *G. speciosa* ($2n = 16$). A partially sterile diploid hybrid gave 200 plants in the F_2 . One of these F_2 plants was triploid and was somewhat similar in appearance to the *G. Tetrahit* occurring in nature. This triploid was crossed with *G. pubescens* and gave one seedling—a tetraploid ($2n = 32$). The tetraploid was perfectly fertile and in all respects similar to the wild *G. Tetrahit*. The artificial *G. Tetrahit* crosses readily with natural *G. Tetrahit* and gives rise to fertile hybrids.

The meiosis of the hybrids between the artificial and wild *G. Tetrahit* shows a preponderance of bivalents, indicating that the chromosomes carried in the tetraploid derived from *pubescens* and from *speciosa* are homologous in part at least with the chromosomes of *G. Tetrahit*. The facts that pairing takes place between the chromosomes of *speciosa* and *pubescens* in the diploid F_1 hybrid and that trivalents are present in the triploid and tetraploid hybrids, indicate that the chromosomes of *speciosa* and *pubescens* have parts in common. Müntzing has gathered a large amount of material together on the subject of sterility in *G. Tetrahit*, and in hybrids with another tetraploid species *G. bifida*, which is presumed to be of analogous or similar origin to *G. Tetrahit*. He is of the

opinion that sterility may be explained on a basis of two factors. It seems possible to us, however, that the sterility is due to inter-homology (*i.e.*, allosyndesis) between chromosomes of two or more of the ultimate diploid parental species.

If allosyndetic pairing occasionally occurs between parts of chromosomes, the pairing properties of the resulting chromosomes in later generations may not be greatly changed but the genetic balance will certainly be influenced. Indeed, Müntzing supposes that the chromosomal constitution of the artificial *Tetrahit* is pr/ps where p and s represent the *pubescens* and *speciosa* complements and r a set made up of recombination products between s and p . Kihara (1930) criticises this assumption of a recombined set of chromosomes, but we are rather of the opinion that if the sterility is chromosomal and not factorial in essential origin, the r set of chromosomes consists of recombinations. This example merits further study along cytological lines.

Triticum. Hybrids of diploid ($2n = 14$) with tetraploid ($2n = 28$) or hexaploid ($2n = 42$) wheats are almost entirely sterile, but hybrids between tetraploids (the *Emmer* group) and hexaploids (the *vulgare* group) are comparatively fertile. F_1 pentaploid hybrids form 14 bivalents and 7 univalents at meiosis. The bivalents disjoin normally while the univalents split longitudinally at the first division and pass at random to opposite poles at the second division. Occasionally laggard univalents appear and are not included in the daughter cells. The gametes therefore contain, in general, 14 + 0 to 7 chromosomes. In agreement with this, Kihara (1919, 1921, 1924), Sax (1923) and Watkins (1924) found F_2 plants with chromosome numbers ranging from 28 to 42.

Kihara (1921, 1924) and Watkins (1924) found that all the expected zygotie series were not obtained and that the F_2 could be divided into two classes—the “diminishing group” and the “increasing group.” The diminishing group consisted of plants containing from 28 to 34 chromosomes which normally formed 14 bivalents and 0 to 6 univalents. (The plants having 35 chromosomes formed 14 bivalents and 7 univalents like the F_1 plants.) The increasing group consisted of plants containing 36 or more chromosomes and the sum of the number of bivalents and univalents

equalled 21. The above plants were normal in vigour and more or less fertile, hence Kihara termed them fertile combinations.

Occasionally dwarf and sterile plants occurred which contained more than 35 chromosomes. The manner in which the chromosomes paired, however, did not conform with that of the "increasing group," e.g., 20 bivalents, or 15 bivalents and 4 univalents were formed. Kihara called these plants sterile combinations.

Kihara (1921, 1924) and Watkins (1924, 1925, 1927 *a, b*) found that on selfing plants of the diminishing group the progeny consisted of plants containing the same number of chromosomes as the parent or a lower number. In later generations 28 chromosome plants were obtained. Similar breeding work with plants of the increasing group gave plants with the same number or a greater number of chromosomes than the parent, and eventually plants with 42 chromosomes were obtained.

It is generally believed that the haploid complement of 14 chromosomes of *Emmer* is homologous with 14 chromosomes of the *vulgare* haploid complement, and therefore 14 bivalents are formed in the F_1 . Kihara and Watkins assume that the 7 unpaired univalents in the F_1 are all different from the other chromosomes in the F_1 . They believe that all fertile combinations must contain 14 E.v. bivalents ($E = \textit{Emmer}$ chromosomes and $v = \textit{vulgare}$ chromosomes) and in addition may contain 1 to 7 of the extra *vulgare* univalents, each univalent being different (the diminishing group and the reconstituted F_1); should any univalents be represented twice, i.e., as bivalents, the remainder of the 7 different univalents must also be present (the increasing group).

Watkins (1924) has calculated the frequency of the various possible combinations, assuming random segregation of the univalents at the second division and allowing for chromosome loss. He has also shown diagrammatically (1930) how plants having less than 40 chromosomes, in the progeny of a plant having 40 chromosomes, would be sterile combinations and how plants having more than 30 chromosomes, in the progeny of a plant having 30 chromosomes, would be sterile combinations.

A true breeding segregate having between 28 and 42 chromosomes will rarely occur and such a form is important genetically. A. A. and

L. A. Sapehin (1928) found a segregate having 36 chromosomes (16 bivalents + 4 univalents) which bred true for chromosome number and morphological characters. This case requires further study in order to find out its chromosome constitution and to account for its behaviour. Thompson and Hollingshead (1927) also found two plants of normal habit which formed 17 bivalents + 1 univalent and 15 bivalents + 4 univalents respectively. According to Kihara's scheme these ought to have been sterile combinations.

Pentaploid wheat hybrids are difficult to analyse genetically since most of the characters segregate in a complex manner. Moreover, there is great variability in many of the characters. Often, indeed, they exceed the limits set by the parental forms and new characters and abnormal types also appear. In the progeny of these hybrids, association of certain characters (types) is common and there has been a tendency to study the inheritance of types rather than single characters.

Watkins (1927 a) obtained similar results to Kihara (1924) and concluded that there was a definite relation between type and chromosome number. Crosses between F_1 (*turgidum-vulgare*) and *vulgare* gave :—

- (1) Plants more than 35 chromosomes which were of *vulgare* type and bred true for this type.
- (2) Plants like the F_1 with 35 chromosomes and which gave *vulgare* and *turgidum* types in the progeny.

Crosses between F_1 (*turgidum-vulgare*) and *turgidum* gave :—

- (1) Mostly plants of *turgidum* type which bred true for this type.
- (2) A few plants having 35 chromosomes.

After studying thirteen pairs of alternative characters, Thompson (1925) was able to group the F_2 into three classes. He concluded that certain characters were associated and association was found to be greatest between those characters which were generally characteristic of the species.

From an economic point of view it is desirable that certain characters should be transferred from one group to the other, e.g., the rust resistant character of the forms with 28 chromosomes to the forms with 42 chromosomes.

Some characters are easily transferred from one group to the other but other characters are seldom transferred. Watkins (1927 *b*), (*turgidum* \times *vulgare*), found that the characters keeled *vs.* round glumes were easily transferred but had no association with chromosome number. The transferring of the rust resistant character, Sax and Gaines (1924) consider as difficult but not impossible. Tochinai and Kihara (1927) found that in the F_4 of a cross, rust resistant (28 chromosomes) \times susceptible (42 chromosomes) the plants with 28 or 29 chromosomes were resistant in a variable degree while all the plants with 42 chromosomes were susceptible. They concluded, therefore, that this character was associated with chromosome number. Other morphological characters were also considered to be associated with chromosome number, *e.g.*, plants of the increasing group never had pithy straw. Similar results with regard to rust resistance were obtained by Hayes, Parker and Kurtzweil (1920), Thompson (1925), Aamodt (1927) and Stevenson (1930).

Occasionally an exceptional resistant *vulgare* type was obtained, Thompson (1925) and Stevenson (1930). Thompson found three plants of *vulgare* type which were somewhat less resistant than the *durum* parent. A few other characters may behave in this way, *e.g.*, solid *vs.* hollow straw. Thompson (1925) and Watkins (1927 *a*).

Sax (1923) (*durum* \times *vulgare*) also found a correlation between five characters and chromosome number. He therefore concluded that the 7 unpaired *vulgare* chromosomes carried the factors for the distinguishing character of the *vulgare* wheats. Thompson (1925) and L. A. Sapehin (1928), however, consider that this conclusion is unjustified. Tochinai and Kihara also suggested that these 7 chromosomes carried the factors which weaken the resistance to rust. On this basis the rare transference of a character may be explained by assuming that one of the 7 chromosomes occasionally pairs with an *Emmer* chromosome.

Watkins (1927 *b*) has attempted to make an exact factorial analysis of *turgidum* \times *vulgare*.

The parents of the F_1 possessed the character waxy foliage and the F_1 plants were also waxy.

The F_2 consisted of waxy and non-waxy plants, the latter being of the *turgidum* type.

The $F_1 \text{ } \varnothing \times \textit{turgidum}$ gave all waxy plants half of which bred true for waxy, while half gave waxy and non-waxy. The F_1 was therefore heterozygous for the factors W waxy and w waxless.

The $F_1 \text{ } \varnothing \times \textit{vulgare}$ gave only waxy plants which bred true for waxy. The unpaired *vulgare* chromosomes were therefore considered to have introduced an extra factor for waxy W^1 .

Watkins explains these results by assuming that the *turgidum* parent has the formula (WW) , and the *vulgare* parent $(ww)W^1W^1$. The factors in the brackets are supposed to be carried by the chromosomes which pair and segregate normally in the hybrid. The factor W^1 is supposed to be carried by one of the *vulgare* chromosomes which are unpaired in the hybrid. He has shown that half of the hybrids, $(\textit{turgidum} \times \textit{vulgare}) \times \textit{vulgare}$, give a few waxless sterile combinations. Thus zygotes $(ww)W^1$ having more than 35 chromosomes would give a few waxless sterile combinations, since they would contain some of the 7 *vulgare* chromosomes which were unpaired in the F_1 , represented twice as bivalents. The plants therefore would not contain representatives of all the 7 unpaired *vulgare* chromosomes and would lack at least the chromosome carrying W^1 . A few $(ww)W^1$ or $(Ww)W^1$ plants having 35 chromosomes, however, would occur. These would give some waxless fertile combinations having less than 35 chromosomes, *i.e.*, *turgidum*-like. Such types were observed by Watkins and Cory (1931).

Good 1 : 1 ratios were obtained by Watkins and Cory in a study of the following characters in the progeny of the F_1 back-crossed with the parental species: rough *vs.* smooth chaff, red *vs.* white chaff, waxy *vs.* waxless foliage, beardless *vs.* bearded ears, and keeled *vs.* round glumes. Linkage was observed between the factors for keeled and bearded. This behaviour indicates that allosyndetic pairing is the rule. If the W^1 chromosome paired with the w chromosome and the W chromosome remained unpaired (autosyndesis) a 1 : 1 ratio would also be obtained. Such pairing is unlikely, since the parental forms are frequently recovered in the back-cross. This evidence also suggests that 11 or 12 of the chromo-

somes of the two species are closely similar. It should be noted later that Watkins has suggested a similar explanation for the chromosome relationships in interspecific *Nicotiana* hybrids.

Watkins and Cory point out that all 28 and 42 chromosome wheats are not expected to have the above formulæ, e.g., *T. spelta* var. White spelt is either $(WW)W^1W^1$ or $(WW)w^1w^1$.

Waxless is a new character which occurred in the F_2 and was associated with low chromosome number in accordance with the above hypothesis.

As already mentioned, Watkins found that the characters keeled and round glumes were not associated with chromosome number and were easily transferred from one species to another. He also found that other characters were transferred to *vulgare* together with keeled glumes thus producing the speltoid—a special type associated with high chromosome number.

The *turgidum* parent had keeled glumes of normal thickness and a moderately dense ear. These characters he regards (1928) as being due to a group of completely linked factors represented by K. The *vulgare* parent had round glumes of normal thickness and a moderately dense ear—k. K is supposed to produce the keel to the glume and to increase the thickness of the glume and the laxity of the ear. k represents the group of recessive allelomorphs to those of the K group.

On crossing the two species 28 KK and 42 kk, two new types also associated with chromosome number were obtained, (1) 42 KK, the *speltoid* type: this is a *vulgare* type having a lax ear and thick keeled glumes which are only pulled away from the grain with difficulty, (2) 28 kk, a *turgidum* type: this has a very dense ear and thin rounded glumes. This interpretation is supported by evidence from crosses between speltoid, *vulgare*, *turgidum* and the F_1 (*turgidum-vulgare*) Fig. 53, p. 277.

Comparison of the two round-glumed types—*turgidum* 28 kk and *vulgare* 42 kk—showed that they differed in other characters. The same applied to the two keeled glume types, *turgidum* 28 KK and speltoid 42 KK. Watkins therefore considers that the unpaired *vulgare* chromosomes have an effect like K and suggests that one of them carries a group of linked factors K^1 . The formulæ given to

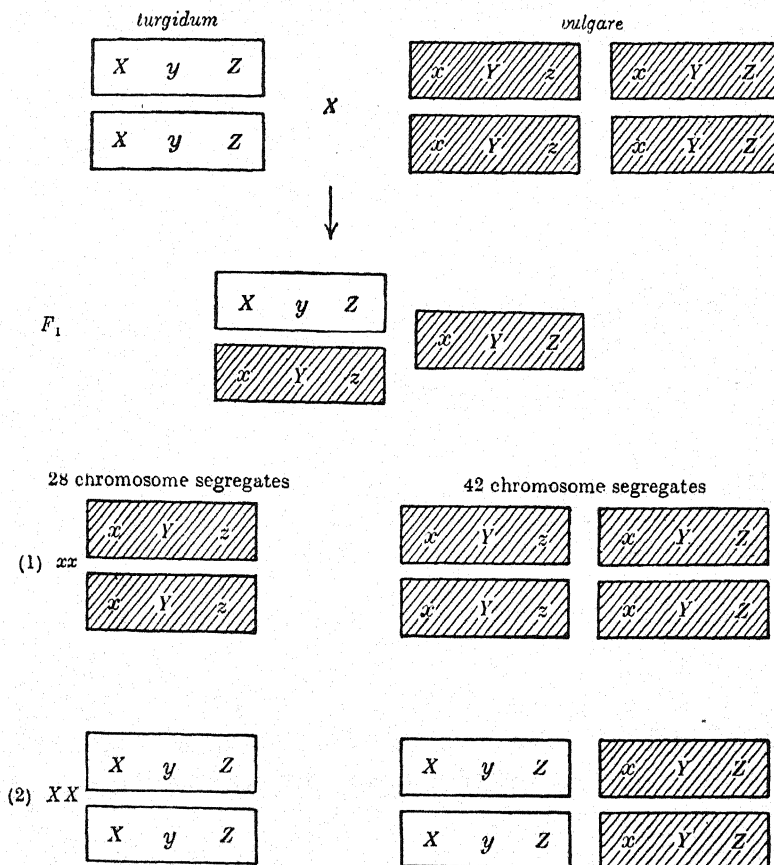


FIG. 54.—Diagram of the association of type with chromosome number. The character determined by \bar{X} is transferable from one species to another. The type is associated with chromosome number, since the 42 and 28 chromosome segregates will differ by Z if both are xx , and by Y if both are XX . (*vulgare* chromosomes shaded). (Watkins, 1930.)

the parents is therefore (KK) for *turgidum* and (kk)K¹K¹ for *vulgare*.

Out of the apparent chaos in segregation of these pentaploid hybrids Watkins has seized upon certain main features—single pairs of characters are often associated with chromosome number, and in

several cases can be transferred from one species to another ; many characters segregate in groups which are probably determined by groups of factors, since separation of these characters occasionally occurs ; types (combinations of characters) are associated with chromosome number ; new types arise, and generally variation exceeds the extremes set by the two parents. He has attempted to explain these in accordance with mendelian principles and with their cytological behaviour.

From his explanation of the inheritance of waxy it seems that the paired and unpaired chromosomes carry a similar series of factors. He therefore assumes that the tetraploid *turgidum* has 2 similar series of factors represented by A_1A_2 , and the hexaploid *vulgare* has 3 similar series $A_1a_2A_3$. This is in agreement with Winge's hypothesis that in these polyploids each of the sets of 7 chromosomes are more or less similar. A_3 is supposed to be carried by an unpaired chromosome. Now, e.g., in the cross $a_1a_2 \times a_1a_2A_3$ the character would be associated completely with chromosome number unless the extra chromosome carrying A_3 paired with one of the others. In the cross $a_1A_2 \times a_1a_2a_3$ the character would be easily transferred. $a_1A_2 \times a_1a_2A_3$ would give rise to a_1a_2 with a new character and to a form $a_1A_2A_3$ where the character might be more highly developed than in either parent. Association between chromosome number and type he explains by assuming that the A symbols represent different groups of linked factors. As an example, he takes the case where the characters keeled and round glumes are not themselves associated with chromosome number but the combination of characters which goes along with them is associated with chromosome number. He shows diagrammatically how keeled and round can be transferred and how the round-glumed 28 and 42 chromosome segregates differ in type and also how the keeled-glumed 28 and 42 chromosome segregates differ in type (Fig. 54).

Nicotiana. Clausen (1928 *a*) recognises twenty distinct species of *Nicotiana*, of which the somatic chromosome numbers are 18, 20, 24, 36?, 48, or 72 (the hybrid *digluta*). The majority of the species, however, have 24 or 48 chromosomes.

Interspecific Chromosomal Relationships. Hybrids between species within each of the three classes, $2n = 18, 20$ and 48 are

fertile and their meiotic behaviour is normal. The following pairing behaviour is found at meiosis in hybrids between certain of these species (Clausen, 1928 *a, b*).

Close pairing	<i>paniculata-rustica</i>	$(2n = 24 \times 2n = 48)$
	<i>sylvestris-Tabacum</i>	$(2n = 24 \times 2n = 48)$
	<i>tomentosa-Tabacum</i>	$(2n = 24 \times 2n = 48)$
	<i>Rusbyi-Tabacum</i>	$(2n = 24 \times 2n = 48)$
	<i>tomentosa-Rusbyi</i>	$(2n = 24 \times 2n = 24)$
Loose pairing	<i>glauca-Tabacum</i>	$(2n = 24 \times 2n = 48)$
	<i>glutinosa-Tabacum</i>	$(2n = 24 \times 2n = 48)$
No pairing	<i>sylvestris-tomentosa</i>	$(2n = 24 \times 2n = 24)$
	<i>glutinosa-Bigelovii</i>	$(2n = 24 \times 2n = 48)$
	<i>sylvestris-Rusbyi</i>	$(2n = 24 \times 2n = 24)$

By intercrossing various species, Goodspeed and Clausen and their co-workers have come to some definite conclusions as to the relationships between the chromosome sets of several species. Fig. 55 shows the cytological behaviour of the F_1 hybrids between these species (Goodspeed and Clausen, 1928; Clausen, 1928 *a, b*; and Brieger, 1930). It also shows the presumed relationships between the different chromosome sets, the manner in which the hybrid *digluta* arose and the probable origin of *N. Tabacum*. Below the diagram is the interpretation of the pairing behaviour of a trispecific hybrid having chromosomes contributed by all three species (*N. Tabacum* \times *N. Rusbyi*) \times *N. sylvestris* (Brieger, 1930).

No pairing takes place among the twenty-four chromosomes in the haploid *N. Tabacum*. This indicates that the two sets of twelve chromosomes are of different phylogeny (Chipman and Goodspeed, 1927; Clausen and Mann, 1924). Further, this confirms the view that the haploid complement of *N. Tabacum* consists of one set of twelve chromosomes corresponding to the haploid complement of *tomentosa* or *Rusbyi* and one set corresponding to that of *sylvestris*. Goodspeed and Clausen (1928) point out that *N. sylvestris* and *N. tomentosa* are morphologically different, whereas *tomentosa* and *Rusbyi* are similar. They assume therefore that *Tabacum* arose by doubling of the chromosomes in a hybrid between *sylvestris* and

tomentosa or close allies of these species. This was followed by genetic differentiation in both the hybrid and the ancestral stocks, but the differentiation was not sufficient to destroy the homology between the chromosomes.

Other cases of a similar type are *Galeopsis Tetrahit*, *G. bifida*, *Salix neocinerea*, *S. Laurina* (Heribert-Nilsson, 1918, and Håkansson, 1929 a), *Phleum pratense* (Gregor and Sansome, 1930, and Gregor, 1931), *Spartina Townsendii* (Huskins, 1930), *Æsculus carnea* (*A. Hippocastaneum* \times *A. pavia*) (Skovsted, 1929), *Rosa Wilsonii* (*R. pimpinellifolia* \times *R. tomentosa*) (Blackburn and Harrison, 1924), *Dahlia variabilis* (Lawrence, 1929, 1931 a) and polyploid wheat and oats (see pp. 218, 225).

The hybrid polyploid forms which have arisen in experimental material, *Primula Kewensis*, *Digitalis mertonensis*, *Saxifraga potterensis*, *Rubus* RT₄, *Solanum nigrum* \times *S. luteum*, *Euchlæna* \times *Zea* (Emerson and Beadle, 1930), *Ægilops* \times *Triticum* (Tschermak, 1926), *Brassica napocampestris* (Frandsen and Winge, 1932) and *Crepis artificialis* (Collins, Hollingshead and Avery, 1929), are also similar; cytological and genetical differentiation might possibly take place in the same way as presumed in the above natural hybrid polyploids.

When the chromosome constitutions of the parental species are known the meiotic behaviour of the chromosomes in the interspecific hybrids can be understood.

It will be noticed that the chromosome behaviour of the hybrids between *digluta* and *Tabacum* or *glutinosa* is similar to that of the hybrids between *Tabacum* and *sylvestris*, *tomentosa* or *Rusbyi* and between *N. paniculata* and *N. rustica* (Goodspeed, Clausen and Chipman, 1926) cf. Fig. 55 and p. 321.

The homology of the chromosome sets in these species leads to characteristic phenomena in relation to fertility, breeding behaviour and survival of the allopolyploids.

For example, the hybrid from *digluta* \times *Tabacum* (*digluta* will not hybridise with *Tabacum* or *glutinosa* when used as a male) is highly fertile, whereas the hybrid from *digluta* \times *glutinosa* is sterile. The homology of the chromosomes in the first case is such that 24II and 12I are formed at meiosis, while in the second case 12II and 24I are

formed (see Fig. 55). The behaviour of the univalents during meiosis (random assortment and occasional elimination—see p. 241) leads to a range in the chromosome numbers of the gametes of the F_1 s. It is also found that the univalents which succeed in entering a gamete are further eliminated by inviability of the gametes. Therefore either by selfing the F_1 , *digluta* \times *Tabacum*, or by crossing it to *Tabacum*, the *glutinosa* chromosomes are eliminated in a few generations (Clausen, 1928 *b*). If *digluta* arose in nature it would remain constant until it hybridised with *Tabacum* when the hybrids would give rise to a preponderance of *Tabacum*-like forms.

Complete pollen sterility is characteristic of the *sylvestris*-*Tabacum* F_1 hybrid. Goodspeed and Clausen (1927 *a*) found that most of the progeny of this cross had from 0–3 univalents in addition to the bivalents and only two plants had all twelve univalents. In the progeny of the *paniculata-rustica* hybrid twelve univalents were frequently found and the univalents were eliminated less frequently. In both cases the behaviour of the chromosomes at meiosis is similar, but the balance and viability of the gametes is different and gives differences in the genetic results.

There are many varieties of *N. Tabacum*, and Goodspeed and Clausen (1917) and Brieger (1928 *b*) found that the morphology of the F_1 hybrid between *Tabacum* and *sylvestris* was affected by the particular variety of *Tabacum* used. The hybrids resemble an enlarged *Tabacum* variety with the addition of some *sylvestris* characteristics. A genetical study of the hybrids can only be made by back-crossing, since they are male sterile. When back-crossed with *sylvestris* two classes were found among the progeny:—

- (1) A large group of highly variable aberrant forms which were almost sterile when selfed.
- (2) A smaller group of forms more similar to *sylvestris* which were partially fertile. Later generations from these plants gave progeny which were completely fertile and identical with *sylvestris*.

In contrast to the original F_1 *Tabacum-sylvestris*, where the chromosomes formed 12 *Ts.S.* bivalents and 12 *Tr.* univalents at first metaphase, the progeny of the back-cross to *sylvestris* would form 12 *SS* bivalents and a variable number of *Ts* and *Tr* univalents.

When the F_1 *sylvestris-Tabacum* was back-crossed with *Tabacum* the progeny could be grouped into three classes.

- (1) A large group of aberrant forms which were sterile when selfed ;
- (2) A few forms like *Tabacum*, which were almost sterile ;
- (3) A few forms like *Tabacum*, which were partially fertile, and among whose progeny were fertile lines identical with the original *Tabacum*.

Any products of recombination formed in the F_1 hybrid are apparently soon eliminated in the succeeding generations.

If p = number of *Tr* univalents eliminated in the gametes of the F_1 ,

q = „ *Ts* „ in the F_1 gamete,
and $12-q$ = „ *S* „ „ „

where p and q = $12-0$, the chromosomal constitution of the progeny of the back-cross F_1 *Tabacum-sylvestris* \times *Tabacum* may be represented thus— $qTsTs$ bivalents + $(12-q)TsS$ bivalents + $(12-p)TrTr$ bivalents + pTr univalents.

We suggest, therefore, that the first class above corresponds to those forms which arise from F_1 gametes containing less than 12 *Tr* univalents and a variable number of *Ts* chromosomes. Class (2) contains those with the majority of *Tr* and *S* chromosomes, while class (3) contains the majority of *Tr* and *Ts* chromosomes.

Goodspeed and Clausen found that *sylvestris*-like derivatives of the *Tabacum-sylvestris* hybrid behaved in a similar manner to that of pure *sylvestris* when further crossed with *Tabacum*. One exception, however, was found. When one *sylvestris* derivative was crossed to the *Tabacum* var. *purpurea* parent which was used in the original cross, half the progeny had the characteristic *purpurea* type of leaf base. They supposed that the *sylvestris*-like derivative from the cross *Tabacum* var. *purpurea* \times *sylvestris* contained a chromosome, or part of a chromosome, derived from the *Tabacum* var. *purpurea* parent.

Watkins (1925) considers that the *Ts* and *sylvestris* chromosomes which pair in the F_1 hybrid are genetically similar, and that the 12 *Tr* chromosomes contain the differential factors for the *Tabacum* species. Replacement of the *Ts* chromosomes by *sylvestris* chromo-

somes therefore will not have a great effect on the phenotype of *sylvestris*-like derivatives. Naturally, where *Ts* and *S* contain allelomorphous factors, replacement will demonstrate this difference, e.g., *purpurea* type of leaf base. In the progeny of the F_1 back-crossed to *Tabacum*, the *Tabacum*-like plants will have obtained (from the F_1 parent) most of the 12 *Tr* chromosomes which carry the special *Tabacum* factors; the aberrant forms will have obtained *Ts* and *S* chromosomes along with one or more of the 12 *Tr* chromosomes from the F_1 parent. The differences in morphological characters are mainly due to the difference in the number of *Tr* chromosomes present.

Webber (1930 b) made a cytogenetic study of a hybrid between *Tabacum* and *sylvestris* which had 60 chromosomes, i.e., the somatic complement of *Tabacum*, $2Ts + 2Tr$ and the haploid complement of *sylvestris*, *S*.

This form was chromosomally unbalanced and gave rise to many new chromosome combinations in the progeny. In appearance it did not differ greatly from its sister triploid F_1s , but was much more fertile. The increase in the proportion of *Ts* and *S* chromosomes in comparison with *Tr* was not, therefore, reflected in the external morphology; the effect of the *Tr* chromosomes gives apparent support to Watkins' view. Evidence, however, has been furnished by Webber that a few of the *Ts* chromosomes contain factors controlling *Tabacum* characteristics.

Later generations from the 60 chromosome hybrid show that elimination of the *sylvestris* chromosomes may or may not be accompanied by phenotypical change. This indicates that the *Ts* and *S* chromosomes may be similar, but not identical, in genetic content.

The production of pink flowers, presumably by exchange of homologous chromosomes between the two species, has been observed in the back-cross (*sylvestris* \times *Tabacum*) \times *sylvestris*, by Goodspeed and Clausen, and in derivatives of the polyploid F_1 *sylvestris* \times *Tabacum*, by Webber.

Later generations of the 60 chromosome hybrid between *sylvestris* and *Tabacum* showed considerable variation in morphology. These plants had generally 24 or 25 bivalents. These differences follow

from multivalent association between the *Ts* and *S* chromosomes and replacement of *Ts* by *S* homologues. The former type of plant might be considered to be a variety of *Tabacum*, but the latter had distinct *sylvestris* characteristics. Hence, as the result of forming a complex polyploid which would not survive in nature, forms can be created, distinct in type, which have a new basic number of chromosomes, and are fertile. In this particular case, the twenty-five bivalent forms would not long remain distinct if in contact with *Tabacum*, since hybridisation would reduce them to *Tabacum*. In isolation, however, such a form might easily become differentiated sufficiently to ensure that when it again came into contact with *N. Tabacum* it would not hybridise.

The hybrids between *N. rustica* and *N. paniculata* show a general similarity in behaviour to the hybrids between *Tabacum* and *sylvestris* and between *digluta* and *Tabacum*, but the particular differences between the first two and the second two examples are of interest.

As a result of the cytogenetic studies of Goodspeed, Clausen and Chipman (1926), Lammerts (1929, 1931) and East (1921) the constitution of *N. paniculata* ($2n = 24$) may be represented as 12 *PP* bivalents and that of *N. rustica* ($2n = 48$) as 12 *RpRp* and 12 *RR* bivalents.

The hybrid forms 12 *PRp* bivalents and 12 *R* univalents at first metaphase and produces gametes containing 12-24 and sometimes 36 chromosomes in frequencies expected on random assortment of the chromosomes. Lammerts and East back-crossed the F_1 with *rustica* reciprocally and found that 32% of the viable egg cells contained the somatic number of chromosomes. On the male side the functional gametes of the F_1 contained 18-24 chromosomes, but gametes with 23 and 24 chromosomes were most frequent. All the plants with 24 bivalents were fertile but were variable in appearance—some resembled the *rustica* parent while others indicated that some *paniculata* homologues had been transmitted from the F_1 hybrid. In addition a range of plants was found with 18 bivalents and 6 univalents to 23 bivalents and one univalent. These plants (246 in number) fell into two groups: (1) a very large group which resembled *rustica* in general characteristics and was equal to or

greater than the F_1 in fertility. (2) Four plants which were almost identical with *paniculata*. Two were sterile and two were fertile.

The third intermediate group corresponding to the intermediate group in the progeny of the back-cross (*sylvestris-Tabacum*) \times *Tabacum* was absent. Later generations from plants in both groups were more fertile and more similar to *rustica* and *paniculata* respectively. It was found that the *rustica*-like group varied in a manner similar to *rustica* itself, which is known to exist in a number of distinct varieties. Indeed, some of these plants resembled particular varieties of *rustica* which had not been used in the cross. Lammerts (1931) has made an extensive cytological examination of these progenies. He found that in viable zygotes the sum of the number of bivalents and univalents formed was equal to the haploid number of the tetraploid parent *rustica*—24. This is similar to Kihara's explanation of the behaviour of hybrid pentaploid wheat derivatives. The F_1 hybrid is of the constitution $RpPR$ and when crossed with *rustica*, which produces gametes containing RP , we expect in the progeny 12 PP bivalents, together with RR and RRp bivalents and R and Rp univalents. As in the *sylvestris-Tabacum* hybrid the relative number of bivalents and univalents depends on the number of R , Rp and P chromosomes transmitted from the hybrid.

The *Tabacum-sylvestris* F_1 is less variable than *N. rustica* and it is probable that the hybrid *rustica-paniculata* will produce more viable and variable progeny than the *Tabacum-sylvestris* F_1 .

The experiments in *Nicotiana*, *Galeopsis*, wheat, oats, *Phleum*, *Primula Kewensis*, *Rubus* and others are informative on several points of biological importance.

The wild species, *Galeopsis Tetrahit*, *Nicotiana Tabacum*, *Nicotiana rustica*, *Phleum pratense* (6x), *Salix cinerea*, *Rosa Wilsonii*, *Spartina Townsendii*, *Dahlia variabilis* and other species are shown to have been evolved by hybridisation and polyploidy.

Most of these forms have chromosomes which are not greatly differentiated from those of the original parents. Where the two original parental species of a polyploid hybrid have no homologous parts of chromosomes the polyploid hybrid will have total

autosyndesis and full fertility. Such forms are *Raphanus-Brassica*, *Nicotiana Tabacum* and *N. digluta*. If a hybrid can be obtained between two species it is probable that these species are related to some extent and have had common ancestors. It is therefore expected that parts of the respective chromosome complements will be homologous since the chromosomes will be of the same origin. Allosyndetic pairing will occur with respect to these parts. Any differentiation of the chromosomes of the parental species which has taken place since the two species originated, may therefore be measured by the amount of allosyndesis occurring in the immediate polyploid hybrid between them. *The amount of differentiation will be inversely proportioned to the amount of allosyndesis.* Thus in *P. Kewensis* one and at most three quadrivalents are formed while in *Galeopsis* artificial *Tetrahit* and pseudo-*Tetrahit* ($3x$), trivalents are formed occasionally, and in the artificial hexaploid of *Phleum pratense* \times *P. alpinum* multiple associations of chromosomes are found.

As already pointed out, allosyndesis in such a hybrid leads to reduction in fertility. Further, crossing-over between homologous parts of otherwise non-homologous chromosomes will lead to the recombination of factors and to interchange, translocation and hence to reduplication and deficiency. Sterility is associated with these chromosomal abnormalities and natural selection will probably eliminate these forms. On the other hand, recombination will enable new balances to be set up which may be favoured by selection on the grounds that they are accompanied by the appearance of a character valuable to the plant. Such may be the cause of the appearance of small flowers in the tetraploid *Galeopsis* when the two diploid and related species have large flowers. Müntzing found that the triploid and tetraploid forms of *Tetrahit* had greater variability in flower size than the parents, but that the natural species had less variation.

The fact that newly-formed polyploids often show greater variability in zygotic and gametic sterility than their succeeding generations may be explained therefore on the above basis. Obviously the degree of homology between the chromosome sets derived from each parent is of great importance in determining the

genetic behaviour of a new polyploid. There may be some polyploid species hybrids which exhibit the phenomena of structural hybridity. The differentiation of the chromosomes of the two parental species may be both genetical and structural. In a polyploid hybrid, the presence of a previous segmental interchange may therefore be brought to light.

Back-crossing a polyploid hybrid with the parental species usually produces a plant with an uneven number of chromosomes. Consequently this hybrid is comparatively sterile and gives rise to progeny ranging in type and chromosome number. Some of these derivatives, however, may have a relatively high survival value. For example, the plants with 25 bivalents which result from the polyploid hybrid between *Tabacum* and *sylvestris* might be the progenitors of several species of *Nicotiana* with a new basic chromosome number. Naturally, of course, the origin and survival value of these forms are dependent on the genetic balance. The difference in behaviour of the hybrids between *N. Tabacum* and *sylvestris* as compared with that of the hybrids between *N. rustica* and *paniculata* is probably due to their different balance.

The gain or loss of a chromosome in polyploids has much less effect on the balance than in diploids. Thus in a polyploid such as *N. Tabacum* aneuploidy might be expected more frequently than in the supposed diploid parental species. Plants with a chromosome deficiency are extremely rare in diploids. $6x - 1$ or $6x - 2$ forms of wheat and oats are known, and Goodspeed and Clausen (1926 a, b) have described two $4x - 1$ forms of *N. Tabacum*. These monosomic forms, "corrugated" and "fluted," were found in a *Tabacum-sylvestris* hybrid and in *Tabacum* respectively. About 60% of the eggs and 3% of the pollen containing the chromosome deficiency are functional. The particular chromosome homologous to that which is deficient in "corrugated" must bear a dominant factor for red flower, since 31% of coloured plants were obtained on crossing "corrugated" with white *N. Tabacum* and 98-100% of coloured forms on crossing normal sister plants with white *Tabacum*. Forms are even known which have no "fluted" chromosome (nullo-*F*) or no "corrugated" chromosome (nullo-*C*).

In a progeny of a selfed haplo-fluted plant which had carmine

flowers (Co) a coral-flowered (co) plant was found (Clausen, 1930). This plant bred true for coral flowers. By crossing normal coral plants with fluted carmine plants the combination fluted and coral was obtained. It will be remembered that "fluted" has the chromosome constitution of 23 bivalents and one univalent. It was found that the univalent contained the alternative factors or factor complexes for carmine and coral. Sometimes in the hybrid between fluted carmine and normal coral a plant was obtained which was variegated for the coral and carmine flower colours. Cytological examination showed that the normal plants had 24 bivalents, the fluted plants 23 bivalents and one univalent, while the variegated plants had a fragment in addition to the complements of normal or fluted plants. This fragment appears to be about one-fifth of the size of the fluted univalent and has been seen to behave irregularly at division of the nucleus. This evidence shows that the fragment is a fragment of the fluted univalent and contains the factor or factor complex for coral and carmine flower colour. When the fragment is present carmine flower colour will be produced but in its absence the coral flower colour will be found in plants with the coral complex on the fluted chromosome. The variegated condition arises through the irregularity of the behaviour of the fragment during mitosis.

If we designate the chromosome which is deficient in "fluted" plants as F and the fragment of F which bears Co as f , the constitution in respect of the F chromosome of the plants can be written:

normal coral (24II) $F\text{-co } F\text{-co}$,

"fluted" coral (23II + I) $F\text{-co}$,

normal, heterozygous carmine, coral variegated plant

(24II + I f) $F\text{-co } F\text{-co } f\text{-Co}$,

"fluted" heterozygous carmine, coral variegated plant

(23II + I + I f) $F\text{-co } f\text{-Co}$.

This example is of great interest since it illustrates the effect of chromosome fragmentation upon factor inheritance and upon variegation in the somatic tissue.

Indeed Clausen (1932) found five wholly carmine plants in the progeny of carmine coral plants. These reversions from a variegated

form, of the constitution $F\text{-}co\ F\text{-}co\ f\text{-}Co$, indicate that in some way Co (carmine) has become stabilised. The reversion of mutated endosperm characters in maize investigated by Stadler (see p. 134), and the behaviour of mutable genes (see p. 145), may be considered along with this case.

Crepis. Genera such as *Crepis*, *Carex*, *Viola*, *Salix* and *Rosa* have been extensively studied from the point of view of species differentiation. In these investigations the genetics, cytology and taxonomy of the species have been taken into consideration. These genera exhibit some of the phenomena already seen in *Nicotiana* as well as characteristics peculiar to each of them.

In *Crepis* and *Carex* changes in chromosome number and morphology are frequent. Chromosome numbers in *Crepis* species include $2n = 6, 8, 10, 12, 14, 15, 16, 22, 33, 40, 44, 55$ and 88 , but about three-fifths of all the species have the somatic number of 8 , and about one-fifth of the species have the chromosome number 10 . *Crepis capillaris* is distinct among the higher organisms in having the low chromosome number $2n = 6$.

At least six interspecific hybrids of *Crepis* have been observed to occur in nature. Certain of these occur not infrequently, and the fact that interspecific hybrids may be obtained artificially with comparative ease indicates that in nature, where different species occur together, hybridisation may not be uncommon. Artificial hybrids in about 100 different combinations involving 36 species have been obtained by various workers. Only about one-fifth of these hybrids are fertile to any extent under natural conditions, and these are mostly hybrids between closely related species. A table compiling results obtained by the various workers is given by Babcock and Navashin (1930). The study of this group of partially fertile hybrids substantiates the close morphological relationships observed between the parental species. Many hybrids which are almost sterile can be back-crossed successfully. In this way it has been possible to study them and their derivatives both genetically and cytologically. In general where one parent has more chromosomes than the other, the characters of the parent with the higher chromosome number predominate in the F_1 .

Collins and Mann (1923) obtained vigorous hybrids between the

species *C. biennis* ($2n = 40$) \times *C. setosa* ($2n = 8$). The F_1 possessed characters mostly resembling *C. biennis* and contained 20 *biennis* chromosomes and 4 *setosa* chromosomes. In meiosis 10 bivalents and 4 univalents were formed regularly, indicating that the chromosomes of the *biennis* haploid complement paired among themselves, i.e., autosynesis. In view of this they predicted the possibility of

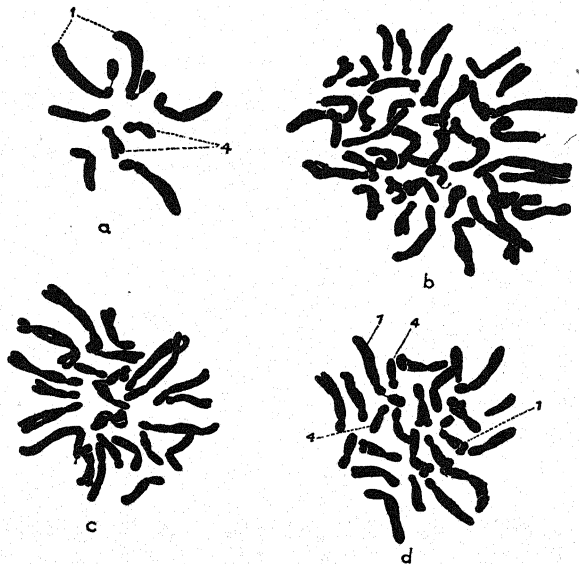


FIG. 56.—Somatic chromosomes of a, *Crepis setosa* ($2n = 8$); b, *C. biennis* ($2n = 40$); c, F_1 hybrid *C. setosa* \times *C. biennis* ($2n = 24$); d, *C. artificialis* ($2n = 24$); the 2 pairs from *setosa* are numbered as in a. (Collins, Hollingshead and Avery, 1929.)

obtaining constant fertile forms containing chromosomes derived from both species. This prediction was fulfilled (Collins, Hollingshead and Avery, 1929). The F_2 plants were very heterogeneous—those most like *biennis* being most fertile. One F_4 plant was found to breed true, and since it possessed characters distinct from other species it was given specific rank and termed *C. artificialis*. It formed a link between two subgenera *Eucrepis* and *Barkhausia*. The chromosome complement of *C. artificialis* was found to consist of 10 pairs of *biennis* chromosomes plus two pairs of *setosa* chromo-

somes. The two pairs of *setosa* chromosomes could be recognised from their morphology (Fig. 56). At first metaphase 12 bivalents were observed—autosyndesis accounting for its breeding true. On back-crossing *artificialis* with *setosa*, it was found that 7 bivalents and 2 univalents were formed in the derivatives, and therefore autosyndesis must have taken place in the case of the 10 *biennis* chromosomes. Further evidence of this form of internal pairing among the 10 *biennis* chromosomes was obtained from the progeny of an F_1 back-crossed with *biennis*. In this case some plants received no *setosa* chromosomes from the hybrid parent, and since 15 bivalents were formed, the 10 *biennis* chromosomes from the hybrid parent must have formed five pairs. From this evidence it is concluded that *C. biennis* is an octoploid species containing eight sets of five chromosomes, although each kind of chromosome is probably not present eight times. The distinctive size and vigour of this species as compared with other species also substantiates the view that it is polyploid. Up to the present no species of *Crepis* have been recognised as the forms from which the polyploid *biennis* may have originated.

In *C. artificialis* we have an example of a new species which has appeared suddenly by hybridisation and not through gradual changes. An essential feature in the meiosis of *C. artificialis* is the autosyndetic chromosome pairing, which results from the polyploid nature of one of the parent species.

Triploids have been observed by Navashin (1925 b, 1926, 1929 a, b) in the following species, *C. capillaris*, *C. tectorum*, *C. dioscoridis* and *C. parviflora*. He believes that they arose by fusion of an egg containing the diploid number of chromosomes, with a normal male gamete. Tetraploids were found in *C. tectorum* and a pentaploid in *C. capillaris*.

On selfing triploids the progeny consisted mainly of diploids and triploids and a few single and double trisomics and higher grades of polyploids. Using these triploid forms as females in crosses with other diploid species, Navashin (1927 b, 1929 a) obtained hybrids containing two, three and four maternal haploid groups along with the haploid paternal group. F_1 interspecific hybrids, when allowed to hybridise with the parental species and when sufficiently fertile,

were found by Navashin (1927 b, 1928, 1929 b) to give mainly triploids and diploid hybrids in the progeny (when a third species is present trispecific hybrids are sometimes produced). A few recombination products and higher polyploids occur. The triploids contain two haploid groups of one parent and one haploid group of the other parent; the diploids are either like the pure parental species or identical with the F_1 hybrid. The higher polyploids may have, for example, three haploid sets from one species with either one or two haploid sets of the other species. In three cases interspecific hybrids containing the diploid complement of each parent have been obtained, viz.,

- 2 *capillaris* + 2 *dioscoridis* (Navashin, 1929b)
- 2 *capillaris* + 2 *tectorum* (Hollingshead, 1930b)
- 2 *rubra* + 2 *fætida* (Poole, 1931).

The latter tetraploid hybrid was the only one which was somewhat fertile—an unusual result, since most polyploid hybrids in *Crepis* and similar tetraploids in other genera are partially fertile.

Trispecific hybrids usually (i.) are gigantic, especially so if they contain two or more haploid sets of one parent, (ii.) show characters of all three species, and (iii.) are sterile.

There is, therefore, no lack of evidence of chromosome doubling, either in the species itself or through hybridisation, and the fact that a tetraploid interspecific hybrid which is somewhat fertile has been produced tends to support the possibility of chromosome doubling having given rise to the higher numbers in the series. On the other hand, when an attempt is made to utilise this evidence in the theoretical reconstruction of the species, it meets with little success.

Among the progeny of a triploid hybrid of *C. capillaris* \times *C. tectorum* Hollingshead (1930 b) found a class containing the diploid *capillaris* chromosome complement together with various combinations of *tectorum* chromosomes. Like trisomics, these were of low viability and tetrasomics did not occur. This evidence is against the idea that species with the addition of chromosomes may arise in this way, but is not conclusive since all species may not behave in this manner.

The genetics of several diploid species has been studied, *C. capillaris* ($2n = 6$), Babcock and Collins (1922 a, b), Rau (1923), Collins (1924), *C. dioscoridis* ($2n = 8$), Collins (1926), Haney (unpub.), *C. fetida* ($2n = 10$), Haney (unpub.), *C. neglecta* ($2n = 8$), Avery (unpub.), *C. rubra* ($2n = 10$), Haney (unpub.) *vide* Babcock and Navashin, 1930, *C. tectorum* ($2n = 8$), Collins, *vide* Babcock (1922), and in each case the pairs of characters were found to segregate in a mendelian manner. Factor mutation has probably played a part in the formation of the numerous polymorphic species in the genus.

The view that factor mutation only produces pathological effects and cannot therefore play a part in evolution is quite untenable, for besides other examples given throughout this book many of the allelomorphic characters studied in *Crepis* have no effect whatsoever on the viability and fertility of the plant.

An interesting contrast is shown by *C. capillaris* where hairy involucre is dominant to hairless involucre, while in *C. neglecta* and *C. bursifolia* for the same characters the dominance is reversed.

On crossing two distinctly different forms of *C. capillaris*, *C. tectorum* or *C. rubra* (Haney, unpub.), respectively, it was found that the F_1 s were only about 50% fertile and the F_2 s were highly variable. This evidence indicates that in species of wide geographic distribution, factor mutation and structural rearrangement may have produced extreme types and this process continuing with the aid of isolation may eventually produce forms of specific rank. Further evidence that factor mutation has played a part in the evolution of *Crepis* was obtained by Collins (1921). On crossing two different races of *C. capillaris* both races having no paleæ on the receptacle (a character which is almost universal in *Crepis*), he found types among the hybrids having paleæ on the receptacle. Moreover, this recessive reversionary character was inherited in a simple mendelian manner. Presence of paleæ is phylogenetically older than its allelomorph, absence of paleæ. It is therefore probable that a step in the evolution of *Crepis* has been made through the dominant factor mutation for absence of paleæ.

An interesting interspecific lethal factor has also been discovered in *Crepis*. Babcock and Collins (1920 a) and Navashin (1926) crossed *C. capillaris* with *C. tectorum* and obtained hybrids which died in the

cotyledon stage. Later Navashin (1927 *b*) succeeded in obtaining viable hybrids, whilst Haney (unpub.), using different plants of each species, obtained five families, one of which produced twenty mature plants, the other four families dying at the cotyledon stage. Hollingshead (1930 *a*) investigated this behaviour and found that some plants of *C. tectorum* contained a factor, either in the homozygous or heterozygous condition, which did not affect the germination, but was lethal to the development of hybrids between *C. tectorum* and *C. capillaris*. This lethal was also effective in hybrids of *C. tectorum* with *C. bursifolia* and *C. leontodontoides*, but probably ineffective in hybrids between *C. tectorum* and *C. setosa* or *C. taraxacifolia*. The races of *C. tectorum* used in this experiment were of wild origin and from regions widely separated so that this factor mutation took place either early or frequently in the evolution of this species.

The cytological study of *Crepis* species, Babcock and Collins (1920), Collins and Mann (1923), Mann (1925), Taylor (1925), Navashin (1925 *a, b*, 1926, 1927 *a, b*, 1928, 1929 *a, b*, 1931 *a, b, c*), Babcock and Mann Lesley (1926), Hollingshead (1930 *b*), Hollingshead and Babcock (1930), Collins, Hollingshead and Avery (1929), Babcock and Clausen (1929), Avery (1930) and Rosenberg (1928), indicates a further method of species evolution—namely structural change of the chromosomes.

By comparing the somatic chromosome complements of different species with regard to their number, morphology and size, some insight is obtained regarding the relationships between the species and the processes which have given rise to the differentiation.

Particular attention has been paid to morphological characteristics of the somatic chromosomes such as the position of the attachment constriction, the presence and absence of satellites and also differences in size. In this way it has been possible to recognise each of the pairs of homologous chromosomes in most of the species.

The majority of *Crepis* species differ from their closer relatives in the morphology of the chromosomes and not in the number of chromosomes. That these morphological characteristics of the chromosomes are constant has been amply proved. Thus in interspecific *Crepis* hybrids it has been shown that the parental

chromosomes appear unaltered in the hybrid. Incidentally, this affords further proof that the chromosomes retain their individuality. A few exceptions to this rule have been discovered which usually consist of the loss of a satellite from a particular chromosome. This phenomenon is termed amphiplasty. An example of this is to be found in the F_1 hybrid between *C. capillaris* and *C. tectorum* where the satellite on the *tectorum* D chromosome is always lost, while the satellite on the *capillaris* chromosome is unaffected. This behaviour occurs whichever way the cross is made. On the other hand, in the F_1 hybrid between *C. capillaris* and *C. parviflora* the satellite is always lost from the *capillaris* chromosome. This behaviour is regarded as the result of the particular physico-chemical condition set up in the hybrid cell.

It has been found that morphologically similar species of *Crepis* have similar chromosomes with which condition is associated a common phylogenetic origin. There is one exception where a group of species far removed phylogenetically have similar chromosomes.

Changes have taken place during the process of evolution with regard to chromosome shape. Races occur within species which differ from the type in the shape of one pair of chromosomes (position of attachment constriction) and others occur which possess a heteromorphic pair of chromosomes. Another species may be divided into three races regarding their chromosomes bearing satellites. One race has two large satellites, one has two small satellites and one has unequal satellites on the pair of homologous chromosomes. These satellites remain unchanged in later generations. This evidence indicates that changes in shape are not uncommon.

Differences in size and number of the chromosomes must also have occurred. Generally increase in number is associated with increase in length. Differences in length may occur with regard to the total length of all the chromosomes (*i.e.*, chromatin mass, for all *Crepis* chromosomes are of about the same thickness) but may only affect individual chromosomes.

Navashin (1931 *b*) has examined thirteen species and found that the cell volume is proportional to the amount of chromatin, *i.e.*, the size of the chromosomes. Thus it was proved that interspecific

differences in the amount of chromatin have the same consequences as intraspecific differences where the diploid complement is increased by one or more haploid complements, *i.e.*, polyploidy.

Alteration in the chromosome number, *e.g.*, the addition of a pair of extra chromosomes does not appear to have taken place following previous non-disjunction since no diploid species of *Crepis* is known to have more than two homologous chromosomes associated. Further, the genetical evidence shows that trisomics are of low viability, and that tetrasomics do not occur. As already seen, however, increase in chromosome number through doubling of the chromosomes is a possibility.

Decrease in chromosome number, *e.g.*, elimination of a pair of chromosomes may result from irregularities at meiosis or from fusion of non-homologous chromosomes. No evidence of the former type is available in *Crepis*, and known cases of this type only occur in polyploids, *Triticum* (Kihara, 1924, 1925; Huskins, 1928 *a*), *Avena* (Huskins, 1927) and *Primula Kewensis* (Newton and Pellew, 1929). The plants moreover were partially or wholly sterile. $2n-1$ plants have never been discovered in *Crepis* and such types in *Datura* never gave rise to plants lacking a pair of homologous chromosomes. Possible evidence of fusion has been obtained in the discovery of a large V-shaped chromosome (Navashin, 1931 *a*).

As has been already pointed out most of the closely related species differ in morphological details of the chromosomes and not in chromosome number. These morphological differences are therefore regarded as being the most important factor in the differentiation of the species. As to how these differences take place the evidence is very meagre. There is no definite evidence for fusion but fragmentation of the chromosomes has been observed in three species of *Crepis*. In certain cases the fragmented chromosome has given rise to two functional chromosomes, and in one species plants containing fragmented chromosomes were partially fertile. In this way new specific chromosome sets may have originated. Large V-shaped chromosomes, which have been observed, have probably resulted through fragmentation and fusion.

Recent cytological investigations in other genera have shown that changes involving, fragmentation, translocation, reduplication,

TABLE 42
List of successful hybridisations. (I, II, III denote univalents, bivalents etc.) (Clausen, 1931 a)

Cross No.	Maternal species	Paternal species	Conjugation of chromosomes in F_1	Fertility, seeds per plant, F_1	Germination	Carried to	Including backcrosses to	F_1 cultivated year	Remarks
1	<i>cornuta</i> $n = 11$	<i>elegantula</i> $n = 10$	ca. $10n + 1_1$ (1-6), III + IV occur	300-500, not poor	poor, 9%	F_2	<i>elegantula</i>	1925	F_3 did not germinate
2	<i>elegantula</i> $n = 10$	<i>Orphanidis</i> $n = 10, 11$	multivalent association (III, IV, V, VI; I rare)	250-300, rather good	—	F_1	—	1930	spontaneous hybrid
3	<i>lutea</i> $n = 24$	<i>elegantula</i> $n = 10$	$14-15n$, 6-41, autosynthesis, polysomic chains formed	50-100, poor	poor	F_2	—	1928	poor flowering of F_1
4	<i>cornuta</i> $n = 11$	<i>orthoceras</i> $n = 11$	$11n$, no elimination	rather good	poor	F_2	—	1927	—
5	<i>Orphanidis</i> $n = 10, 11$	<i>cornuta alba</i> $n = 11$	$8-11n$, 8-01, III and IV occur	200-400, rather good	poor, 10-20%	F_2	—	1927	F_3 weak
6	<i>tricolor alba-yellow</i> $n = 13$	<i>elegantula</i> $n = 10$	$8-10n$, 7-31, polysomes (III-VI) rather common	abt. 30, very poor	—	F_4	<i>elegantula tricolor</i>	1927	segregated cespitose, sterile dwarfs
7	<i>tricolor alba-yellow</i> $n = 13$	<i>Orphanidis</i> $n = 11, 10$	$0-11n$, 24-21, some III and IV; I split often	$30-130$, poor	poor, 24%	F_4	<i>tricolor</i>	1927	—
8	<i>tricolor alpestris</i> $n = 13$	<i>alpestris</i> $n = 13$	$13n$, rarely 2-41; extranuclear nucleoli very common	1500-2000, very good	abt. 60%	F_2	—	1926, 1928	3 different reciprocal crosses

9	<i>tricolor</i> n = 13 <i>arvensis</i>	<i>arvensis</i> n = 17 <i>tricolor</i>	11-13n, 8-4i	500-2000, very good	good	F ₉	<i>tricolor</i> , <i>arvensis</i>	1921 and later	11 different reciprocal crosses
10	<i>tricolor alba</i> n = 13 <i>Kitaibeliana</i> n = 7	<i>Kitaibeliana</i> n = 7 <i>tricolor alba</i> n = 13	4-6n, 12-8i, occasional III	0-30, very poor	—	F ₁	<i>tricolor</i> , 10-30 seeds per plant	1930	—
11	<i>tricolor alba</i> n = 13	<i>Kitaibeliana</i> n = 18	7-12n, 17-7i, non-reduction observed, I split often	20-50, very poor	not good, 23%	F ₂	<i>tricolor</i>	1927	—
12	<i>tricolor alba</i> n = 13	<i>nana</i> n = 24	5-1i, (= 16-18n), III and IV occur; autosynesis	1000-2000, very fertile	—	F ₁	<i>tricolor</i>	1930	—
13	<i>tricolor alba</i> -yellow n = 13	<i>rothomagensis</i> n = 17	ca. 1iv, 2-3ni, 3-6i (+ bivalents), splitting, elimination	12-37, very poor	poor, 15%	F ₄	<i>tricolor</i>	1927	—
14	<i>tricolor hortensis</i> n = 13 <i>lutea</i>	<i>lutea</i> n = 24 <i>tricolor</i>	8-11i, mostly splitting conjugation often in irregular chains	50-300, rather poor	poor, 10%	F ₄	—	1925	<i>tricolor</i> , <i>alba</i> × <i>lutea</i> less viable
15	<i>tricolor hortensis</i> n = 13 <i>Battandieri</i>	<i>Battandieri</i> n = 26-30 <i>tricolor</i>	few I; autosynesis; III + IV	ca. 100, rather good	not good, 25%	F ₂	—	1927	<i>tricolor alba</i> -yellow × <i>lutea</i> less viable
16	<i>arvensis</i> n = 17	<i>rothomagensis</i> n = 17	4-6i, often splitting; 1-2ni, occasional IV; (+ II)	250-450, rather good	30%	F ₂	—	1926-1928	reciprocal un-successful
17	<i>Kitaibeliana</i> n = 7	<i>arvensis</i> n = 17	most common: 6ii + 12i; up to 2n + 20i; many I split	500-600, rather good, but reduced	poor, 18%	F ₂	—	1926	—

TABLE 42—continued

Cross No.	Maternal species.	Paternal species.	Conjugation of chromosomes in F ₁ .	Fertility, seeds per plant, F ₁ .	Germination.	Carried to	Including backcrosses to	F ₁ cultivated year.	Remarks.
18	<i>nana</i> n = 24	<i>arvensis</i> n = 17	2-6 _{II} , 37-29 _I ; occasional one III	250-800, rather good	—	F ₁	—	1930	—
19	<i>Kitaibeliana</i> n = 18 n = 7	<i>Kitaibeliana</i> n = 7 n = 18	abt. 6 _{II} + 13 _I ; sometimes one III	ca. 100, very poor	very poor ca. 3%	F ₂	—	1929	—
20	<i>nana</i> n = 24	<i>Kitaibeliana</i> n = 7	5-6 _{II} , 21-19 _I ; III + polysomes occur	250-300, not poor	—	F ₁	—	1930	—
21	<i>nana</i> n = 24	<i>lutea</i> n = 24	15-18 _I ; polysomic conjugation	50-300, rather poor	—	F ₁	—	1930	—
22	<i>lutea</i> n = 24	<i>Battandieri</i> n = 26-30	—	50-100, not good	50%	F ₂	—	1923	—
23	<i>Battandieri</i> n = 26-30	<i>calcarata</i> n = 20	—	16-60, poor	poor	F ₂	—	1929	—
24	Cross 7, F ₁ n = 13 × 11, 10	Cross 1, F ₁ n = 11 × 10	—	33-325, variable	variable	F ₂	—	1928	quadruple hybrid
25	Cross 7, F ₁ n = 13 × 11, 10	Cross 1, F ₁ n = 24 × 26-30	—	130-150	poor	F ₂	—	1928	quadruple hybrid

inversion and deletion of parts of the chromosomes have taken place in the processes of evolution. These changes have also been artificially induced in *Crepis* (Navashin, 1931 c) and in other plants by irradiation with X-rays. It would appear that in the evolution of *Crepis*, changes such as these, termed "transformation," have played an important part, resulting in differences in size and shape and to some extent in the number of chromosomes. Associated with these differences there would naturally be differences in external morphology through loss or gain of factors giving rise to a new factorial balance. In addition, factor mutation would play a part in the differentiation of the species without causing alteration of the chromosome complement. Polyploidy and interspecific hybridisation are also apparently involved in the creation of new species.

Transformation, however, is regarded by the *Crepis* workers as being the most frequent cause for the origin of new species of *Crepis*.

Viola (vide Clausen, 1931 a). In the *Melanium* section of *Viola* are species with chromosome numbers ranging from $2n = 14$ to $2n = 60$, with intermediate numbers such as 20, 22, 26, 34, 36, 40 and 48.

Some relatively fertile interspecific hybrids have been obtained and by a genetic and cytological study of the group it has been possible to indicate in some measure the mode of evolution of the sub-genus.

Table 42 gives the cytological behaviour together with the fertility of some of the species hybrids. It can be seen that hybrids between species with different chromosome numbers were quite frequently obtained and that the F_1 s were sometimes fertile (e.g., the F_1 of *V. tricolor* \times *V. arvensis*) and that succeeding generations were obtained. The chromosome behaviour in meiosis in the species hybrids is of particular interest. In crosses 1, 2, 3, 5, 6, 7, 10, 12, 13, 15, 16, 18 and 20, associations of more than two chromosomes were observed. In addition, several cases were noted where the chromosomes might be considered to be secondarily associated (see p. 233) although Clausen is unwilling to be definite on the matter.

It is of importance to note that multiple association of chromosomes occurred in the F_1 s when only bivalents were formed

in the parent species. An example of such a case is the F_1 of *V. cornuta* ($2n = 22$) \times *V. elegantula* ($2n = 20$), in which trivalents and quadrivalents were formed. Probably this results from differences in the arrangements of the segments of the chromosomes, i.e., the species hybrid is also a structural hybrid.

In other cases where the chromosome number of the hybrids is higher it is probable that both interchange and reduplication of chromosome parts are the causes of multiple association. The presence of univalents may arise either from too little or too much homology among the chromosomes. Trivalent formation or, when the frequency of chiasmata is low, failure to form trivalents or quadrivalents will lead to the appearance of univalents at metaphase.

Autosynopsis sometimes occurs in hybrids between species with high chromosome numbers and species with low chromosome numbers (hybrids, numbers 3, 12 and 15). In these cases, more bivalents are formed than expected from the number of chromosomes in the species with the low chromosome number (cf. *Papaver*, p. 233). It is interesting to note that in three crosses (numbers 7, 11 and 18) the hybrids showed least pairing between chromosomes although the chromosome numbers of the species are comparatively high. From these cytological observations it is possible to estimate the chromosome relationships of the different species. It is seen, for example, that the hybrids involving *elegantula* ($2n = 20$), *rothomagensis* ($2n = 34$), or *lutea* ($2n = 48$), probably contain most multiple associations of chromosomes while the chromosomes of *nana* ($2n = 48$) are not capable of autosynopsis in a species hybrid.

A cogent scheme for the chromosome constitution of the species can be formulated.

diploid, AA	.	.	.	<i>V. Kitaibeliana</i>	.	.	.	$2n=14$
tetraploid, AABB	.	.	.	<i>V. tricolor</i> , <i>V. alpestris</i>	.	.	.	$2n=26$
hexaploid, AABBCC	.	.	.	<i>V. arvensis</i> , <i>V. rothomagensis</i>	.	.	.	$2n=34$
				<i>V. Kitaibeliana</i>	.	.	.	$2n=36$
octoploid, AABBCCCC	.	.	.	<i>V. nana</i> , <i>V. lutea</i>	.	.	.	$2n=48$

In the above scheme each letter represents a set of six chromosomes. It will be noticed that there is no constant basic number x

of the sub-genus, nevertheless, the forms with the haploid numbers 7, 13, 17 and 24 appear to bear some resemblance to a group with the haploid series 6, 12 and 18. Possibly the change from the euploid to the aneuploid series is directly responsible for the various specific differences that have been noted between the forms. The change in balance by the addition of a chromosome, probably derived by duplication, would create a morphological and physiological change sufficient to isolate the new form from the old, in the wild state. The change in chromosome content in an additive manner is apparently common in this sub-genus and it occurs even in one species.

V. Kitaibeliana, to which group *V. nana* belongs, is an instructive example of evolutionary change. The species is known in two forms ($2n = 14$) and ($2n = 36$), which are morphologically very similar although their chromosome numbers do not conform to a geometrical series. Further, hybrids between them show as much if not more, failure of chromosome pairing as in hybrids between taxonomic species. The form *nana* is more compatible with the *arvensis* group than with its own *Kitaibeliana* group.

On cytological grounds alone one is able to say that these various species are related closely to one another and that they have evolved by segmental interchange, polyploidy and hybridisation as in other genera. The evolutionary processes of *Viola* are in contrast to those of *Nicotiana* due to the fact that the aneuploid condition is more viable in *Viola* than in *Nicotiana*. *Crepis* probably occupies an intermediate position in this respect.

The genetical study of *Viola* fully confirms, and also extends, the conclusions derived from the cytological study of the forms. Much painstaking work has been done by Clausen in identifying the various factors involved in the inheritance of flower colour, anthocyanin distribution, shape and size of flower, presence and absence of labellum, and length of life. These factors may be transferred from one species to another by hybridisation and an extraordinary range of phenotypes can be produced. Characters such as labellum and size of flower, which systematists justly use for classification, are inherited in a similar way to varietal differences. As expected from the cytological constitutions, polymeric factors are common

in the group. This is especially the case in regard to the factors controlling anthocyanin production. Other factors, however, are sometimes not duplicated. "Addition, subtraction, duplication and exchange of entire chromosomes or parts of them may account for many deviations from an identical behaviour by chromosomes of species with the same chromosome number." (Clausen, 1931 *a*, p. 300.)

The taxonomic criteria of morphological difference and inter-sterility for species delimitation are certainly difficult to maintain in face of the experiments on *Viola*. Phylogeny may not be appealed to, since the phylogeny of the *Melanium* violets is probably similar to a network rather than to a branching tree.

The manner of evolution of some species in this section has probably been repeated in the production of the species *V. phænoelegantula*, *V. crassicaulis*, *V. hyperchromatica* and *V. velutina* which are forms that have only arisen from species hybrids in culture. The first has 25-27 chromosomes, and arose from *V. tricolor alba* ($2n = 26$) \times *V. elegantula* ($2n = 20$). The second has 25-26 chromosomes, and arose in the F_2 from *V. tricolor alba* ($2n = 26$) \times *V. Orphanidis* ($2n = 22$). *V. hyperchromatica* ($2n = 42$) arose from the cross *V. tricolor* ($2n = 26$) \times *V. arvensis* ($2n = 34$). The increased number of chromosomes resulted from partial doubling of chromosomes during meiosis in the F_1 plant. These forms are very fertile and constant for distinctive characters, but variable in others, although their chromosome numbers range round the numbers given above. (Clausen, 1931 *b*, has found that plants of *Viola canina* L., from different districts, have varying chromosome numbers.)

Antirrhinum. The genus *Antirrhinum* may be considered as a contrast to the genera *Crepis*, *Nicotiana* and *Viola*, which contain species whose evolution is bound up with chromosomal change either in number or structure.

Antirrhinum contains at least eight species (Baur, 1910, 1924), and innumerable wild and cultivated varieties. These species, with the exception of *A. siculum*, cross readily and produce fertile progeny. *A. siculum* produces partially sterile progeny on hybridisation with other species of the same genus. Baur (1924) and Lotsy

(1913) have investigated the progeny of several species crosses. The reciprocal crosses between *A. majus* and *A. glutinosum* (*molle*) give rise to F_1 hybrids which are similar and intermediate between the parent species in morphology. The F_2 generation exhibits extraordinary variation; nearly every character is found to vary and to be combined in innumerable ways with other characters. Further, the range in variability of the F_2 exceeds that of the parental species. Teratological flower types which sometimes resemble the flowers of other genera of the Scrophulariaceæ are not uncommon.

The cytological behaviour of these hybrids is unknown, but the parental species have sixteen somatic chromosomes. Since the F_1 hybrids are fertile and produce a great range of types in the F_2 , it is probable that the chromosomes of the F_1 pair as bivalents, and that the factors are able to cross-over as in the parental species, thus giving rise to great variation.

Nicotiana Langsdorffii, *N. alata* and *N. forgetiana* behave similarly to the *Antirrhinum* species. Doubts are sometimes raised as to whether specific rank should be given to such a group of plants which do not normally cross, but appear to have homologous parts of chromosomes and allelomorphic factors. On this point, Lotsy (1916) and Jordan (1905) have attempted to show that the genotype (biotype) is the basic unit which should have specific rank. While the genotype is certainly a basic unit, it does seem that the *Linnaean* species, which is composed of several biotypes, has a definite recognisable position as a biological unit.

CHAPTER X

CONCLUSIONS

Conclusions. The Species Problem.

A GENERAL survey of the trend of plant genetics indicates at once several view points which are strikingly different from those of the last decade and from those held by animal geneticists. The most important change has been brought about by the realisation of the extensive distribution of polyploidy and of the behaviour of forms with multiple associations of chromosomes. The behaviour of polyploids has been harmonised with that of diploids by modification of the hypotheses originally put forward before polyploidy was properly appreciated.

On one hand, greater attention has been directed to the cytological processes by which the genetical factors segregate, and on the other hand, the physiological effects of factors have been more intensively analysed. The structural basis of heredity has been firmly established, while the biological outlook on genetic factors has assumed much greater importance.

Without the cytological information on polyploids and structural hybrids, it would have been extremely difficult to have understood their behaviour. Recently such information has become available, giving rise to genetical interpretations of importance not only to polyploids, but also to normal plants and animals.

The most prominent experiments, involving both cytology and genetics, include those of McClintock upon *Zea*, Stern and Dobzhansky on *Drosophila melanogaster*, Blakeslee, Belling and Farnham on *Datura*, Sömme, de Winton and Haldane, and Darlington on *Primula sinensis*, and Lawrence on *Dahlia variabilis*.

The theory of the specificity of pairing of homologous parts of chromosomes put forward first by Belling and Wenrich, and more precisely by Darlington (1931 a), permits many genetical and cyto-

logical facts of diverse nature to be brought into use in the general testing and confirming of the now well-established chromosome theory of heredity. Structural hybrids such as *Oenothera* with involved genetical behaviour are no longer interesting exceptions, but may be used for furthering the general theories applicable to other plants.

Combined with the confirmation of the chromosome theory of heredity has been the suggestion of the chiasmatype theory of Janssens, Belling and Darlington. It will be noticed that we have given great importance to this theory although it has not yet received universal support. This has been done since we are convinced that no other theory so far produced will explain so many facts of chromosome pairing in such a satisfactory manner. We are also convinced that, although it may be modified in the future, the essentials of the theory are correct.

Cytology is now entering a new phase where statistical methods are being used and where the finer corollaries to the general theory are being tested. The near future will furnish statistical data which must be considered along with genetical data (see p. 97).

In this chapter we are not so much concerned with the more mechanical aspects of polyploidy as with its influence upon biological thought. It should, however, be pointed out again that in the polyploid a gamete may not be pure for one factor, but may contain two or more allelomorphs of that factor. The purity of the gamete is one of the basic principles of mendelism, but on consideration it will be realised that the mode and principle of segregation as defined by Mendel, includes polyploid segregation. Therefore the differentiation of mendelian segregation of factors in diploids from segregation in structural hybrids and polyploids is one of degree and not of principle.

A criticism formerly raised by non-genetical workers, that geneticists were more concerned with the cataloguing of factors and the raising of hypotheses of segregation than with the biological importance of factors to plants, can no longer be maintained. It was said that the genetical worker analysed the factors concerned with non-vital characteristics such as colour or height, and when he found interpretation difficult he introduced a "lethal" into the formula!

Later work has shown that factors are bodies of unknown constitution situated at definite points on the chromosomes. One factor produces something which in reaction with the products of many other factors gives rise to a particular characteristic of the plant. In consequence of the long chain of reaction processes the relation of factor and character is remote. One factor has manifold effects on many characters, but for identification purposes is considered in relation to the most easily identified. For example, tallness *vs.* dwarfness in peas, tomatoes and sweet peas (two allelomorphs identified) is based on a monofactorial difference. Tallness is obviously brought about by many observable characters, such as length of each internode, proportion of tissue laid down, rate of growth, etc. In addition there must be many unobserved differences between tall and dwarf plants. The contrasting factors, however, are necessary for the series of processes to take place. Realisation of this general phenomenon together with the knowledge of a greater number of factors affecting almost all parts and functions of the plant (*cf.* Haldane, 1932) have led geneticists to the view that the physiology, morphology and ontogeny of the plant depend on the reactions of the heritable factors with the environment.

In other words, the geneticist is analysing the basic centres of influence upon which the characteristics of the plant ultimately depend.

Consequently the effect of the factor will vary from one controlling a non-essential character to a characteristic which is vital to the plant. Factors are known which control the pairing of chromosomes at meiosis (Beadle, 1930, 1931, 1932; Darlington, 1931 *a*), the development of endosperm (Mangelsdorf, 1926), pollen tube growth (see p. 14), chlorophyll development (see p. 56), transpiration, formation of reproductive organs (Phipps, 1928; Emerson, 1921, etc.), as well as those controlling size, form and colour. It is only by their differences that the factors are identified. Many which are essential to life are homozygous throughout the species as the result of natural selection and therefore cannot be detected. Nevertheless, the large number of lethal and sub-lethal factors which occur in almost all plants and animals are the allelomorphs of vital factors. Generally the lethal factor produces a reaction process which is

unfavourable to the development of the products of other factors in an early stage. Generally the rapidity of the lethal effect is such that the physiological cause of death can rarely be identified. There are some factors, however, whose effect can be determined, *e.g.*, those causing Tunicate ear in maize and chlorophyll deficiencies. We therefore suggest that some factors are lethal only because their allelomorphs perform some essential or vital action.

Thus we come naturally to the well-known fact of the reactions of the products of one factor with that of another (see p. 34). This has been loosely called interaction of factors when in reality it is meant that the products formed by one factor interact with those of another and the external environment to give the observed result.

Factor interactions and balance can be seen in the diploid, but attention is more sharply drawn to them when polyploids are considered. Several striking examples such as the pod structure of *Raphanus-Brassica* hybrids, the chromosomal globe mutants in *Datura* and various trisomics of *Datura*, tomato and *Matthiola* illustrate well the general influence and importance of a stable balanced constitution to the life of the plant. It will be realised at once that different balances of factors in one species lead to morphological and physiological characteristics similar to those associated with single factors. The normal as opposed to the fluted characteristic in *Nicotiana* is dependent on a fragment of the chromosome associated with the factor for coral (see p. 325). The slender character in *Matthiola* depends on the presence of an extra piece of the A chromosome to the normal nuclear content. Lethality in gametes or zygotes is expressed in various degrees of strength in unbalanced forms. It should be noted also that a plant containing a deficiency is more likely to be non-viable than one containing reduplications; $2n + 1$ forms are much more frequent than $2n - 1$ forms.

Dominance of one factor over another as seen in the character expression is another phenomenon of balance. On pp. 137-162 were described the various theories on the constitution of the factor. The theories are all in agreement on two points. The first is that the dominant factor produces a more saturated condition of

character expression than the recessive in the presence of a given genetic constitution. The second is that the saturation point in character expression may be varied by a change in factors other than the allelomorphs involved.

Particular emphasis is given to these views by the experiments in polyploids. A factor which is completely dominant in a diploid (**A** dominant to **a** in an **Aa** plant) may not attain the same degree of dominance in a tetraploid until in the duplex condition. Either the balance of dominants to recessives in a simplex form (**Aaaa**) is insufficient, or the balance of **A** factors to the quadruple sets of non-allelomorphic factors is disturbed: the saturation point of the character is not reached until more **A** factors are present.

The examples from *Primula sinensis*, *Dahlia variabilis* and *Funaria hygometrica*, quoted in Chapter 5, are of particular interest in this respect. The increase in the number of dominant allelomorphs of one factor results in an increase in the expression of the character controlled by the factor. When the stage of saturation of the character expression has been reached, little or no effect of addition of further dominant allelomorphs will be noticed. This saturation point is not reached in the case of the factor **B** of *Funaria hygometrica*, even in the quadruplex condition, but the expression of capsule colour is probably saturated at a point between the duplex and triplex condition of factor **C**.

Although the heterozygous diploid is intermediate between the homozygous dominants and recessives, the recessive allelomorphs to the **B** and **C** factors in *Funaria* appear to have little influence on character expression in the presence of the dominant. Nevertheless the recessive allelomorphs do exert an effect on the expression which is similar in kind but less in degree than the dominants. This is seen in the fact that **c₄** and **b₄** give rise to character expressions more similar to the appearance of a simplex or even duplex in a tetraploid than to the corresponding triploid and diploid recessives.

An extremely informative example is that of *Drosophila melanogaster*, where Stern was able to produce the expression of the dominant allelomorph by duplication of the recessive allelomorphs (see p. 200). Further he proved that factors in other chromosomes influenced the degree of expression of these duplicated recessive

allelomorphs. The experiments of Lawrence on *Dahlia variabilis* (see p. 200) indicate that, in addition to the interaction of the products of factor action, there must be considered the competition between the factors for materials necessary for their respective products.

He found that the factors **Y** and **I** for production of flavones interfere with the production of anthocyanins by the factors **A** and **B**. **Y** also interferes with the action of **I**. The analysis of various combinations of these factors in the double autotetraploid *Dahlia variabilis* shows that there is an effect proportional to the number of dominant allelomorphs of each factor present.

Dominance and epistasy are the result of the factors interacting with each other, together with the action of environmental factors upon the development of the organism. It will be seen, therefore, that, starting with the analysis of single factors, genetics has built up a coherent scheme which resembles the biological outlook of workers in other biological fields. The advantage in the genetical method lies in the fact that it has established a unitary basis for the biological standpoint.

Several theories appertaining to factors and their action (Fisher's theory of dominance, Goldschmidt's physiological theory and the work of Bridges) as well as the work on polyploids and the mathematical analysis of populations have approached the problem from different angles. The first appreciation of the results of these different lines of approach may indicate differences in outlook, but further consideration shows that the fundamental views are very similar.

Following the Darwinian epoch it was thought that selection could continuously change a race by the aggregation of small mutations directly induced by the selection. This conception was a direct result of Darwin's "Origin of Species" and of Galton's "Laws of Inheritance." Point was given to this view by the knowledge that selection of the best individuals in a species could improve the varieties of the species.

Johanssen, however, showed that selection could only change races which were genetically heterogeneous and had no effect on those which were homozygous. An account of his work on selection

in the weight of beans will be found in Babcock and Clausen (1927).

The consequences of Johanssen's work are important. They show conclusively that selection cannot change the genotype of an individual, but can only eliminate some of the segregates of a heterozygous plant and thereby purify the race into one consisting of plants all alike and homozygous for genetical factors. Selection has no direct effect on the genotype, but only affects the genotype of a race through the phenotypic expression.

Johanssen's work also shows a means of purifying a race and creating a so-called "pure line." By inbreeding and selecting one particular phenotype which is known to correspond to a factor in the homozygous state, purity can be obtained for that factor in a few generations. Jennings (1916, 1917) showed that if the original plant was of the heterozygous constitution Aa the proportion of zygotes of the different genotypes after n generations of self-fertilisation would be:—

$$AA \frac{2^n - 1}{2^n + 1} \quad Aa \frac{1}{2^n} \quad aa \frac{2^n - 1}{2^n + 1}.$$

Hence, after six generations of selfing, the proportions of homozygotes of the constitutions AA or aa would be 98.4% in place of 50% in the first generation (virtually the F_2). If selection eliminated the aa forms the race would be 98.4% pure for AA forms. Jennings (1916, 1917), Haldane and Waddington (1931), etc., Robbins (1918) and Wright (1921 *a, b*, 1930) have examined the problem of different types of mating and different rates of selection in a population and have obtained interesting results.

Even in the diploid the attainment of pure lines homozygous for several factors is difficult, and in practice pure lines involving all the factors of the diploid plant have rarely been obtained. One means of obtaining pure lines is that of breeding diploid progeny from a haploid plant as in *Solanum Lycopersicum* (Lindstrom, 1929). The descendant diploid is presumed to have all the allelomorphic pairs identical. But even here the possibilities raised by positional effect, such as in Bar eye of *Drosophila melanogaster* or mosaicism, Muller (1930 *b*) (see p. 153), and the occurrence of factor mutations

and unusual crossing over between chromosomes in certain haploids (see p. 259), make it problematical as to how many generations from the haploid generation remain pure for all the factors.

The difficulties in creating pure lines of diploids by normal breeding are increased by such complications as lethality, complementary factors, and balance; phenotypes are created in which the heterozygosity of a known or unknown factor is not suspected until outcrossing is performed or inviable gametes or zygotes are observed, *e.g.*, balanced lethals (see p. 52). For example, *Pisum sativum* may be breeding true for green pod but may be of the constitution **aB**, **Ab** or **ab** where **A** and **B** are two complementary factors for purple pod.

Further, although a race may be homozygous for a factor, it may yet be segregating for factors modifying that factor. These cannot be isolated in practice since their effect is small. Hence a character controlled by a principal factor which is homozygous and by modifying factors which are heterozygous may show considerable variation as well as the expected fluctuation. This phenomenon is to be seen in wheat and oats and has been critically proved in *Drosophila obscura* by Koller, 1932.

In polyploids these difficulties are accentuated by the greater number of possible heterozygotes and by their higher rates of segregation. For example, a duplex autotetraploid on being selfed gives only one recessive in 36 plants, while a triplex autotetraploid **AAAa** generally does not segregate. In the latter case the recessive factor remains protected by the dominant from the action of selection until it appears in the progeny of a tetraploid of lower factorial denomination, such as the segregating duplex and simplex forms (see p. 183).

In allopolyploids with constant autosyndesis it is impossible to obtain purity for some factors, *e.g.*, *Primula Kewensis* (see p. 178) and "shift" (see p. 212). By the peculiar chromosome behaviour the recessive factor never segregates until allosyndetic pairing takes place as a rare occurrence (see p. 216). Allopolyploids with constant autosyndesis and also structural hybrids (see p. 263) therefore breed true although they may be heterozygous.

The theory of pure lines is important as a principle in the con-

sideration of other matters and is useful in practice in creating stocks homozygous for a few definite factors.

THE SPECIES PROBLEM

A general survey of species from the genetical standpoint indicates that the change from one type to that of another is more simple than was at one time thought. Hybridisation, factor mutation and structural alteration of the chromosomes in combination with polyploidy give great opportunity for variation. The fundamental nature of balance as the limiting factor of the extent to which change can take place is seen by comparison of the manner in which such genera as *Antirrhinum*, *Crepis*, *Viola*, *Nicotiana*, *Pyrus* and *Drosophila* have evolved. One species may be able to withstand the dropping out of a chromosome, while another would not. The progeny of hybrids between two species may have great variability while others may be relatively constant. A particular example of this difference in hybrids is seen in the contrast between the genetic behaviour of the hybrids *N. Tabacum* \times *N. sylvestris* and *N. rustica* \times *N. paniculata*. The variability can arise either as the result of genetic variability in the parental species or as the result of allosyndesis and chromosome change in the polyploid derivatives.

The last ten years have seen a considerable change in the attitude expressed in the genetical literature upon the subject of species and their origin. The definition of a species is still extremely difficult, and we must rely upon the working classification of the taxonomists.

Instead of it being easier, it is more difficult to define a species at the present time than before. As Anderson (1928) points out, the delimitation of a species of *Iris* differs from that of species of *Aquilegia* (Anderson and Schafer, 1931) primarily because of their different modes of life. In one, the principal means of propagation is vegetative while in the other it is sexual. The primary cytological, genetical and ecological behaviour of the species is even more important in delimiting species than the secondary physiological properties. Huskins pointed out that two species cannot be differentiated on their inability to form fertile F_1 plants as was formerly supposed. On one hand the F_1 hybrid between *Raphanus* and *Brassica* is perfectly fertile. On the other hand, diploid and

tetraploid plants of a single species may only cross with difficulty and the F_1 plants so produced are nearly sterile. Indeed, one and the same plant of the tomato may have fertile diploid and tetraploid parts (see p. 169) which are practically inter-sterile. One race of a species may become practically sterile through segregation of a recessive factor which interferes with normal meiosis (Beadle, 1930, in maize) or with pollen divisions (Beadle, 1931). Mendelian incompatibility factors in *Nicotiana* and cherries are further examples of such sterility.

The various genetical monographs on *Nicotiana* (East, 1928), *Crepis* (Babcock and Navashin, 1930), *Viola* (Clausen, 1931 *a*), *Salix* (Heribert-Nilsson, 1918), *Galeopsis* (Müntzing, 1930 *a*, 1931, 1932 *a*, *b*), which include the results of experiments involving two or more species of one genus have shown conclusively that the taxonomic arrangement of the species is in general a natural one. Further, cytogenetics and ecology have shown that the taxonomic criteria employed in species classification have a biological foundation and are not altogether arbitrary. Thus the taxonomist has isolated the constant and similar features from the dissimilar and variable features in different groups of individuals—a process which involves field study or its equivalent. These constant features are based on identical or homologous factors in the species of one group (*cf. Viola*, p. 339). The homozygosity of the more constant features arose through selection acting on an ancestral mixed population. Hence the taxonomist has chosen the more actively selected features on which to base his classification and in so doing has analysed the results of genetical and ecological processes.

The experiments mentioned above also indicate that in order to analyse the more intricate species relationships in those genera which are known to be difficult, and to obtain a better understanding of the status of the species, it is necessary to combine field study with cultural and genetical experiments. An interesting case where from ecological and physiological points of view genetics has aided the elucidation of species relationships is that of Gregor and Sansome (1930) and Gregor (1931) in *Phleum*. The British *Phleum pratense* will not cross with the American *Phleum pratense*, but both will cross with *P. alpinum* from the mountains in Scotland. The

forms of habit in the two varieties of *P. pratense* are parallel, and no reasons for separation of the varieties from one another were apparent until an examination of the chromosome complements was made. British *P. pratense* had 14 chromosomes and was diploid, while the American *pratense* had 42 chromosomes and was hexaploid. *P. alpinum* had 28 chromosomes and was tetraploid. Gregor hybridised *P. pratense* ($2n = 14$) with *P. alpinum* ($2n = 28$) and obtained a hybrid with 21 chromosomes. This hybrid gave 4 viable seeds from about 500,000 flowers. These four seeds gave rise to plants with the hexaploid number of chromosomes $2n = 42$, and which were cross-fertile with the American variety of *P. pratense*. Hence by outcrossing one variety of *P. pratense* to another species, a hybrid was obtained which was fertile with the other variety of *P. pratense*. It is believed by American botanists that *P. pratense* is not indigenous to America, but was introduced about the seventeenth century from Europe, where *P. alpinum* and *P. pratense* are both found. It may be that these workers have repeated under controlled conditions the process by which the hexaploid American variety was formed in nature. Similar species synthesis is probably that carried out by Müntzing in *Galeopsis*, where a form similar to *G. Tetrahit* was produced by hybridisation.

The following forms have been artificially obtained and have been accepted as species: *Crepis artificialis*, *Nicotiana digluta*, *Saxifraga potternensis*, *Digitalis mertonensis*, *Primula Kewensis*, and many others, all of which show a strict delimitation from the original species. They have arisen by hybridisation and doubling of the chromosomes.

There are other cases of new forms arising by factor mutation, such as in *Drosophila melanogaster* (see Muller, Paterson and Muller), or *Datura Stramonium* (Blakeslee), where factor mutations have occurred in the immediate descendants of a haploid. Distinct forms arise by reduplication, chromosome loss or other cytological abnormalities (*Drosophila*, *Datura*, *Nicotiana*, *Crepis*).

The origin of new forms can therefore take place in many ways. The establishment of these forms, however, is a case where selection plays an all important part. The question as to whether new forms arise either by hybridisation or by mutation is no longer in doubt,

since both methods are known to occur. The important step for the future is to determine how the forms, once they have arisen, are established as ecological units. The flora of Australia is of great interest in this respect, according to the late Professor A. A. Lawson. Here the endemic flora consists of well-defined isolated species, while the incursive flora is hybridising and giving rise to many new types, which are gradually driving the endemic plants to more restricted habitats.

An insight into the methods by which species are delimited one from another by natural selection has also come with the accumulation of knowledge as to the manner of origin of species. From a study of these methods of delimitation it should be possible to obtain criteria for the natural classification of species. A species is produced and remains constant as a distinct form under the strict control of natural selection which acts not as a creative agent but as a choosing agent.

The main processes in the evolution of a species are (1) creation of material on which selection may act; (2) isolation by geographical or physiological causes from related species; (3) selection of characters necessary for survival under the requirements of the habitat in which the plant is placed. The first two processes do not require further attention at this point; they are dependent upon the genetical and cytological background of the species. The third process is one of environmental selection of the available characters provided by the first process. Naturally, the possibility of obtaining the ideal form to suit the environment depends on the results of process (1)—the production of new and heterogeneous material by quantitative or qualitative change. Ecology is the study of the third process.

The importance of combined genetical, ecological and taxonomic work cannot be over-emphasised. Attempts have been made by various workers (Bonnier, Massert, Warming and Clements) to study the life of plants in their natural environments and under diverse conditions. Insufficient attention to the heritable constitution of the plants involved, however, impairs the value of their work. It is only by observing the reactions of a particular genetic constitution to different environments that the agents of natural selection and

physiological isolation may be identified. Without the knowledge of the genetic constitution, variability of more than one plant of any species cannot be reduced to environmental influence alone. Turesson (1921-1931) in Sweden, Marsden-Jones and Turrill (1930), and Gregor (1930, 1931) in Britain, and Anderson (1928) in America, are the pioneers in this combined ecological and genetical work, termed genecology by Turesson (cf. Barton-Wright, 1932). Valuable work on interspersing known races of one species in different environments is being done in Russia by Sukatschew (1928).

The following discussion of Turesson's work (1922, 1923) will indicate that taxonomic species (*linneons*) have a natural constancy and status which does not justify their abolition as natural units. Turesson transferred individuals of a number of plant species from various localities in Sweden to the common environment of the experimental garden. Observations were made on the changes brought about during at least two years' culture upon the morphology of the individuals, and breeding methods were used to show the genetic constitutions of the plants concerned. Wherever a different ecological type of environment occurred, such as cliffs, dunes, etc., along the coast of Sweden it was found that there was a genetically distinct variety of the species which was suitable for the environment. For example, the zone between the cliff and dune regions contained a population of plants consisting of individuals of the neighbouring regions together with hybrids between them. Seeds and plants of species, such as *Hieracium umbellatum*, *Centaurea jacobea*, *Atriplex* spp. and many others, were collected and studied in culture. It was found that the distinct characteristics of a population from the different ecological habitats retained their distinguishing features to such an extent that Turesson could say, by examination of the plant, from which district and which habitat it came. In many cases these characteristics were shown to be inherited. When hybrids were made between two plants from different habitats the heterogeneity of the progeny resembled that of the wild population found in the intermediate zones between two definite ecological habitats.

It was sometimes found that the characteristics of the population from one extreme habitat were accentuated under cultivation *

(breadth of leaf in *Hieracium umbellatum*), while in others the population that appeared uniformly dwarf in the wild varied in heritable habit and height differences when under culture. The explanation, of course, is that the response of a certain genetic constitution to the selective action of environment is different in different plants. A factor for dwarfness and its allelomorph for tallness may not have a great range in character expression in one species, while in another species the variability of the expression may be great. Hence, in the first case, selection of the phenotype will adversely affect one factor, while in the second case, where the phenotypic range of one genotype is great, the differential selection between two factors will be less intense.

The attempt, however, to interpret the correspondence between habitat and habitat-type of the inhabitants as an adaptational process must be carefully analysed in order to avoid too great a generalisation. It is evidently the genotypical constitution of the plant which determines its survival in any habitat. In what manner does a suitable genotype come to be present in a particular habitat for which it is entirely suitable? For example, the prostrate form of *Hieracium umbellatum*, which is found on the stationary beaches, is not found on the neighbouring moving dunes where it is replaced by a form with much stronger shoot regeneration (probably being more able to resist being covered by moving sand). It is not necessary in this book to give further evidence that the environment does not directly create suitable characters (inheritance of acquired characters).

In some parts of Sweden the dune type of plant is not present, although the less differentiated inland form is present, while in other districts the dune type is found. Evidence from plants gathered from several different habitats in one region of Sweden indicates that they are related to one another since they possess several characters in common, such as leaf shape, which are not of primary ecological importance.

Thus we are driven to the conclusion that varieties suitable for survival in an extreme habitat are selected out of the population of the immediate undifferentiated regions.

The population of a cliff in one district has descended from the

population of inland plants in the neighbourhood and has not migrated from a cliff in a different district. This view is entirely opposed to the well-known migration theory but is closely similar to an older theory of polygenesis and can be extended to many examples of geographic distribution. As a result of this analysis of wild populations the *linneon* has been split up into smaller ecological units, each based on genetical considerations. These units in many cases may correspond to the biotypes of Jordan (1905), or the Hagedoorns (1921). Nevertheless we feel, as Turesson does, that to limit the term "species" to such biotype units is to strip the species *linneon* of its characteristic quality, that of being able to react genotypically to a wide range of ecological requirements without losing its general common morphology.

The discovery of the biotype or separate genotype has provided a basic unit from which to build up a composite structure, the *linneon*, but it has not destroyed the value of the *Linnaean* species. We are therefore of the opinion that a real biological basis founded on the combined use of ecology and cytogenetics can be provided for the species of the taxonomists.

It is apparent that despite many mistakes made by taxonomists in admittedly difficult genera (*Rosa*, *Rubus*, *Hieracium*, etc.), their classification of plants has been fully supported by biological investigations. If this genecological basis of taxonomic classification were manifestly adopted, instead of implied, considerable advances in both the vexed question of species and problems of evolution would be forthcoming.

In conclusion, genetics has furnished definite proof of several methods by which evolution can take place. Factor mutation, hybridisation and chromosome rearrangement all probably play a part in the origin of new forms. No longer can the criticism be raised that simple rearrangement of material due to hybridisation cannot give rise to such evolutionary progress. The knowledge that there is a vast unidentified store of factors in all organisms and that different balances between them have such large effects rather suggests that possibly genera or even orders contain approximately the same content of factors in different arrangements; similar mutations in different species of the same genus, such as in rodents

and carnivora (Haldane, 1927) in *Drosophila*, *Triticum* and *Avena*, indicate that there may be a considerable amount of genetical material in common. In addition, factor mutation is always adding new possibilities to the genotype which in some cases may not have an important function until a rearrangement in nuclear material takes place (*Oenothera* is a striking example). The survival of these new types will depend on the action of natural selection and isolation, either geographical or physiological.

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